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Barry Kent MacKay

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AFFINITIES OF THE SAW-BILLED HERMIT (*RAMPHODON NAEVIUS*) DETERMINED BY CYTOCHROME-*B* SEQUENCE DATA

ROBERT BLEIWEISS,[1,4] SHER L. HENDRICKSON,[2] MARK E. BERRES,[2] YOSHIKA O. WILLIS,[3] AND EDWIN O. WILLIS[3]

ABSTRACT.—We sequenced 912 bp of the cytochrome-*b* gene to examine phylogenetic relationships of the enigmatic Saw-billed Hermit (*Ramphodon naevius*), a large and distinctive hummingbird endemic to tropical forests of southeastern Brazil. Bootstrapped maximum parsimony and maximum likelihood analyses of sequence data from 11 hummingbirds and several outgroups (two swifts, one goatsucker) support: (a) monophyly of the traditional hermit (Phaethornithinae) and nonhermit (Trochilinae) subfamilies, (b) placement of *Ramphodon* among hermits, and (c) a sister relationship between *Ramphodon* and an exemplar of the widespread polytypic hermit genus *Glaucis*. The association of *Ramphodon* with derived hermit lineages is concordant with subfamilial patterns of wing anatomy and nest architecture. However, the unusual plumages (striped underparts) and male bills (long, serrated, hooked) shared by *Ramphodon* and the Tooth-billed Hummingbird (*Androdon aequatorialis*) appear to have evolved within separate hermit and nonhermit "tooth-billed" clades. Distal placement of the *Ramphodon-Glaucis* clade within hermits implies that even distinctive Brazilian endemics such as *Ramphodon* are derived forms that evolved relatively recently. *Received 18 March 2002, accepted 6 August 2002.*

Hermit hummingbirds are common inhabitants of forest interior throughout the Neotropics. The distinctive appearance of hermits has led to their designation as a subfamily within the Trochilidae since the first systematic treatments of hummingbirds (Reichenbach 1854, Cabanis and Heine 1860, Gould 1861, Ridgway 1911). However, the intrafamilial affinities of the enigmatic Saw-billed Hermit (*Ramphodon naevius*), a large and distinctive form endemic to the humid lowlands of southeastern Brazil (Ruschi 1986, Grantsau 1988, Sick 1993), have been the subject of considerable debate (Monroe and Sibley 1993, Hinkelmann and Schuchmann 1997, Gerwin and Zink 1998, del Hoyo et al. 1999). In particular, the taxon presents a mosaic of features typical of both the hermit (Phaethornithinae)

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FRONTISPIECE. Saw-billed Hermits (*Ramphodon naevius*) perched (male) and hovering (female) among the native food plant *Centropogon cornutus* (Lobeliaceae). The remarkable bill dimorphism and other superficial characteristics of *R. naevius* combine attributes of both main hummingbird lineages (hermits and nonhermits). Analysis based on DNA sequences reveals that *R. naevius* is a surprisingly derived member of the hermit subfamily. Painting by Barry K. MacKay.

TABLE 1. Taxa and samples used in this study (see Appendix 1).

Common name	Scientific name	Material	Phylogeny reference
Saw-billed Hermit	*Ramphodon naevius*	blood	this study
White-tipped Sicklebill	*Eutoxeres aquila*	frozen tissue	Bleiweiss et al. 1994b
White-whiskered Hermit	*Phaethornis yaruqui*	frozen tissue	Bleiweiss et al. 1994b
Band-tailed Barbthroat	*Threnetes ruckeri*	frozen tissue	Bleiweiss et al. 1994b
Bronzy Hermit	*Glaucis aenea*	frozen tissue	Bleiweiss et al. 1994b
Green-breasted Mango	*Anthracothorax prevostii*	blood	Sibley and Ahlquist 1990
Green-throated Carib	*Eulampis holosericeus*	EtOH-tissue	Bleiweiss et al. 1997
Purple-crowned Fairy	*Heliothryx barroti*	frozen tissue	Bleiweiss et al. 1997
Sparkling Violet-ear	*Colibri coruscans*	frozen tissue	Bleiweiss et al. 1997, Gerwin and Zink 1998
Green-fronted Lancebill	*Doryfera ludovicae*	frozen tissue	Bleiweiss et al. 1997, Gerwin and Zink 1998
Tooth-billed Hummingbird	*Androdon aequatorialis*	EtOH-tissue	Bleiweiss et al. 1997, Gerwin and Zink 1998
Moustached Treeswift	*Hemiprocne mystacea*	EtOH-tissue	Bleiweiss et al. 1994a
White-collared Swift	*Streptoprocne zonaris*	frozen tissue	Bleiweiss et al. 1994a
Common Nighthawk	*Chordeiles minor*	frozen tissue	Bleiweiss et al. 1994a[a]

[a] Representative in same family (Apodidae) as taxon used in earlier study.

and nonhermit (Trochilinae) subfamilies (Monroe and Sibley 1993; Bleiweiss et al. 1994a, 1994b, 1997; Gerwin and Zink 1998). The dull plumage, modest sexual dichromatism, and long bill of *Ramphodon* all are features typical of hermits (Sazima et al. 1995, Hinkelmann and Schuchmann 1997). However, the striking tooth-like serrations and terminal hook on the bill of male *Ramphodon*, as well as bold streaking on the underparts of both sexes, are features atypical for hermits but found to varying degrees among nonhermits (del Hoyo et al. 1999; see frontispiece). Indeed, *Ramphodon* bears a striking resemblance in plumage and bill form to the Tooth-billed Hummingbird (*Androdon aequatorialis*), a monotypic genus that several studies based on molecular (Gill and Gerwin 1989, Monroe and Sibley 1993, Bleiweiss et al. 1997, Gerwin and Zink 1998) or behavioral (Schuchmann 1995) data place among the nonhermits.

Recent morphological studies based on the patagial muscle complex of the wing (Zusi and Bentz 1982) and on cladistic analysis of a suite of external features (Hinkelmann and Schuchmann 1997) suggest that *Ramphodon* is a hermit. However, they differ in placing *Ramphodon* as a basal (external morphology) or more derived (wing anatomy) member of that subfamily. By contrast, some standard linear classifications place *Ramphodon* among the nonhermits, probably because of its morphological similarities to *Androdon* (Monroe and Sibley 1993). In this paper, we use cytochrome-*b* sequence data to assess relationships of *Ramphodon*. In particular, we address three questions about *Ramphodon*, including (a) subfamily membership, (b) placement as a basal or derived taxon, and (c) affinities with respect to similar-looking hermits (*Eutoxeres*) and putative nonhermits (*Androdon*).

MATERIALS AND METHODS

Study materials.—Considerable background information on hummingbird systematics allows judicious selection of taxa for the purpose of comparing hypotheses based on DNA sequencing with those suggested by earlier studies; except for *Ramphodon*, all taxa examined herein were included in earlier studies based on different molecular methods (Table 1). We chose single representatives from each of the four traditional hermit genera (*Eutoxeres*, *Phaethornis*, *Threnetes*, *Glaucis*; Monroe and Sibley 1993) as well as five species from the basal group of nonhermits (mangoes, subfamily Trochilinae; Bleiweiss et al. 1997). We used two levels of outgroups (Table 1) to root the phylogeny, including two representatives from the sister group to hummingbirds (swifts), and one representative from the next most distant clade, a goatsucker (Common Nighthawk, *Chordeiles minor*; Bleiweiss et al.

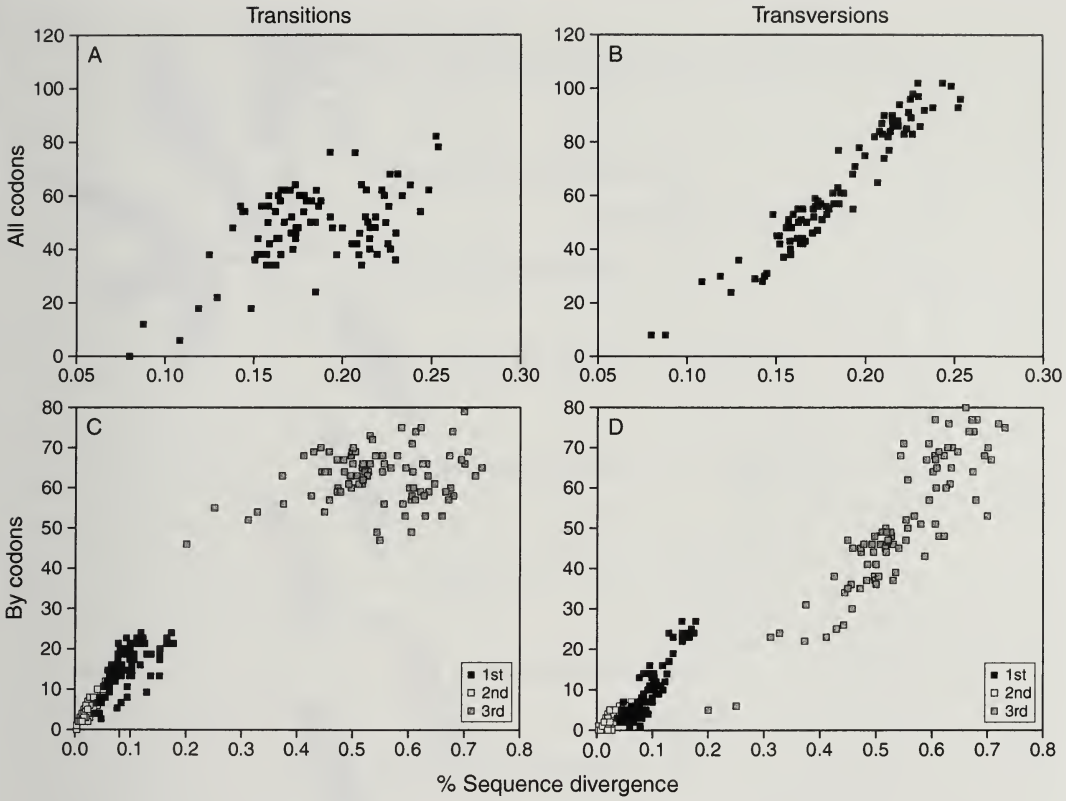

FIG. 1. Plot of the empirical numbers of transitions and transversions (y axis) versus total uncorrected (Kimura two-parameter) pairwise percentage differences estimated in MEGA (Kumar et al. 1993) for all (A, B), and individual (C, D), codon positions across all variable sites across all hummingbird and outgroup taxa.

1994b). Most authors conducted Brazilian field work (RB, MEB, YOW, and EOW), whereas collection of remaining materials was as described previously (Table 1; see also Bleiweiss et al. 1994a, 1997; Appendix). Subsets of authors executed laboratory work (RB and MEB) and analyses (RB and SLH). Specimen information and sequences have been deposited in GenBank (accession numbers AY150649–62).

Mitochondrial cytochrome-b gene isolation and sequencing.—We extracted DNA using Qiagen Tissue Kits (Valencia, California), following manufacturer's protocols. We sequenced single individuals from all taxa, using the polymerase chain reaction (PCR) to amplify the target fragment of the cytochrome-*b* gene with L14841 [5′-CCATCCAACATCTCAGCCATGATGAAA-3′] as forward (Kocher et al. 1989), and H15767 [5′-ATGAAGGGATGTTCTACTGTTG-3′] as reverse (Edwards et al. 1991) primer (numbers follow those for the human mitochondrial genome; see Edwards et al. 1991). The 100-μl reaction volume used for initial PCR comprised 1.0 μg of template, 2.5 units of Taq DNA polymerase (Promega Corporation), and concentrations of 200 μM dNTPs, 1.5 mM $Mg,^{2+}$ and 0.2 μM primer. We amplified the target sequence over 40 cycles in a Perkin-Elmer thermal cycler programmed to optimize yield of the desired product. We visualized reaction products by preparative-gel electrophoresis in TAE buffer, followed by staining with ethidium bromide. Then we used Wizard™ PCR preps to purify amplified DNA either cut from the gel or aliquoted directly from the reaction mixture. Finally, we submitted the amplified DNA product for automated sequencing (Iowa State DNA Sequencing and Synthesis facility) by dye-terminator reactions.

Phylogenetic analysis.—We examined rel-

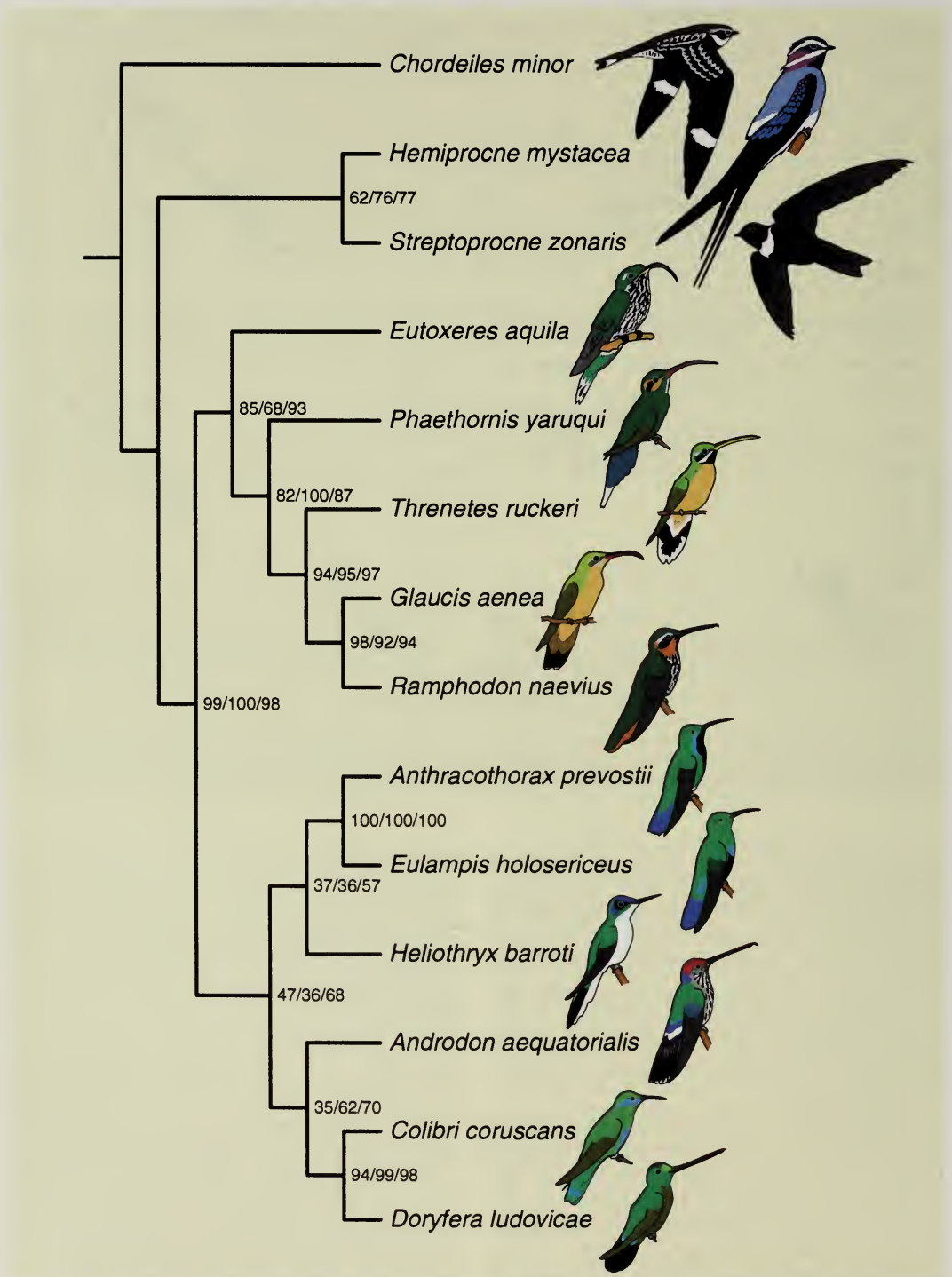

FIG. 2. Bootstrapped topology obtained by maximum parsimony and maximum likelihood for cytochrome-*b* gene sequences for all 14 taxa (rooted to the outgroup goatsucker, *Chordeiles minor*). Numbers at internal nodes indicate percentage bootstrap support out of 100 resamplings: unweighted parsimony (tree length = 1045)/ weighted (codon 1–3 positions = 2:4:1; Ti:Tv = 3:1) parsimony (tree length = 2,300)/likelihood (log likelihood

ative substitution rates with respect to substitution type and codon position by constructing standard plots against Kimura two-parameter (uncorrected) pairwise distance measures of sequence divergence. We plotted both transitions (Ti) and transversions (Tv) separately across all sites, and by codon position. We did not fit regressions through these plots because the points are not independent, but used them to assess qualitatively the need to incorporate possible saturation (multiple substitution) effects through weighting schemes in phylogeny estimation.

We employed PAUP* (ver. 9.0 Beta; Swofford 2002) to conduct all phylogenetic analyses, implementing both maximum parsimony and maximum likelihood methods based on heuristic searches with 10 random addition and 100 bootstrap replicates. Maximum parsimony trees specified a range of weighting schemes: either unweighted (1:1), or weighted for codon position (1st:2nd:3rd = 2:4:1) and transition-transversion ratios (2:1 or 3:1). We used the program MODELTEST (ver. 3.06; Posada and Crandall 1998) to determine the most appropriate model of DNA sequence evolution for use in maximum likelihood analysis. MODELTEST computes likelihood ratio tests (Kishino and Hasegawa 1989; Huelsenbeck and Crandall 1997) first on nested models of DNA substitution from the simplest (Jukes and Cantor 1969) to more complex (Rodríguez et al. 1990) and then on models of the most appropriate of these substitution matrices nested with respect to addition of parameters for invariant sites (I) and the gamma distribution of rates for variable sites (G). Through these series of steps, the program identifies the model of DNA sequence evolution that minimizes parameters without a significant (here based on the program's default $P < 0.01$) improvement in likelihood scores.

RESULTS

Sequence evolution.—No insertions or deletions were detected when sequences were aligned to chicken (*Gallus gallus*) cytochrome-*b* (Desjardins and Morais 1990). Observed base compositional (Prager and Wilson 1988) patterns (estimated in MEGA; Kumar et al. 1993) across all sites (A = 27.5%, T = 25.5%, C = 33.5%, G = 13.6%) and for each codon position were similar to those reported for other birds and vertebrates. In particular, there was little bias at first position (A = 25.2%, T = 23.6%, C = 28.7%, G = 22.5%), slight enrichment in C and under-representation in G at second position (A = 19.5%, T = 39.6%, C = 26.7%, G = 14.1%), and enrichment of A and C with very little G at third position (A = 37.6%, T = 13.2%, C = 45.0%, G = 4.2%).

Pairwise empirical numbers of substitutions across hummingbirds and outgroups (Fig. 1) revealed expected substitution-rate heterogeneity for this mitochondrial gene (Brown et al. 1982, Lanyon and Hall 1994). Transition (Ti) substitutions saturated above approximately 15% level uncorrected total pairwise differences (Kimura two-parameter model; estimated in MEGA) whereas transversions (Tv) remained linear over the observed range (Fig. 1A–B). Among codons, base substitutions accumulated fastest at third position and slowest at second position for both Ti and Tv (Fig. 1C–D). Most of the departure from linearity was contributed by sites at the more rapidly evolving third codon position, for which Ti divergence plateaued or even dropped beyond about 30% divergence (Fig. 1C). The nonlinear portions of curves were comprised almost exclusively of the hummingbird-to-outgroup (swifts, goatsucker) comparisons. Thus, models that incorporate weightings and distinct rate categories are justified.

Specific features of the amplified DNA and

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= −5572.63). Number of parsimony-informative sites ranges from 272 to 282, depending upon the model. Cartoons are based on the following sources: *Chordeiles minor*, *Hemiprocne mystacea*, *Ramphodon naevius*, *Anthracothorax prevostii*, *Eulampis holosericeus*, *Androdon aequatorialis* (del Hoyo et al. 1999); *Streptoprocne zonaris*, *Eutoxeres aquila*, *Phaethornis yaruqui*, *Threnetes ruckeri*, *Glaucis aenea*, *Colibri coruscans*, *Doryfera ludovicae* (Hilty and Brown 1986). Note scattered placement of large-bodied species (*Ramphodon*, *Eutoxeres*, *Androdon*) with large, specialized bills and striped underparts. Birds are not drawn to scale.

its genetic composition also argue that the mitochondrial sequences reported herein do not include ones that underwent atypical change after translocation to the nucleus (Arctander 1995). Only a single gene product of the predicted size ever resulted from our amplifications. Moreover, variation at first and second codon positions did not indicate a relaxation of constraints on the acceptance of substitutions, as would otherwise be expected for a noncoding pseudogene translocated to the nucleus. Rather, the aligned sequences revealed patterns of codon specific and base specific (transition bias) substitution patterns typical of avian mtDNA sequences. Furthermore, the gene sequences were translated in full using the chicken mitochondrial code (Desjardins and Morais 1990), without nonsense or intervening stop codons. The possibility remains that some of the sequences could be recent translocations to the nucleus, in which case insufficient time may have passed to alter the mitochondrial characteristics of the pseudogene. Nevertheless, congruence between sequence and nuclear (DNA hybridization) data in regard to phylogenetic placement of most taxa (see Discussion) provides strong collateral evidence against nuclear contaminants among the mitochondrial sequences.

Phylogenetic analysis.—Bootstrapped 50% majority-rule consensus trees (plus other groups compatible with that tree) for unweighted and weighted parsimony analyses produced the same topology (Fig. 2). An identical topology was obtained for the bootstrapped 50% majority-rule consensus tree for likelihood analysis based on model selection and parameter values determined by MODELTEST; likelihood ratio tests indicated that our data are best fit by a general-time-reversible substitution matrix (6 substitution types, R[A-C] = 0.9109, R[A-G] = 5.4224, R[A-T] = 1.1972, R[C-G] = 0.5601, R[C-T] = 9.5556, R[G-T] = 1.0000), in which the proportion of sites assumed not to vary was 0.4745, and in which rates for variable sites followed a gamma distribution with a shape parameter of 0.9175 (model = GTR + I + G). Bootstrap values for both parsimony and likelihood generally were similar in terms of absolute and relative support among nodes (Fig. 2). Support for internal nodes was higher overall for likelihood, and for hermits compared to nonhermits, but all analyses agreed on level of support and placement of *Ramphodon*.

With the Common Nighthawk specified as the root, the deepest branches among the apodiform taxa indicate monophyly for swifts (two species from two families) and hummingbirds (11 species from across both subfamilies). *Ramphodon* groups with representatives of the other four traditional hermit genera (Sibley and Ahlquist 1990). Moreover, a sister-group relationship between *Ramphodon* and the single exemplar of *Glaucis* within hermits is strongly supported (92–98% bootstrap support across methods). Indeed, all nodes within the derived hermit clade receive very strong support ≥82%), thereby bolstering placement of the *Ramphodon-Glaucis* pairing as a relatively distal lineage within the subfamily. *Ramphodon* showed more distant affinities with the other two taxa (*Eutoxeres*, *Androdon*) that share some of its more distinctive attributes (in plumage and bill morphology). *Eutoxeres* always defined the first split within extant hermits, which separated it from *Ramphodon* by several other branching events within hermits. *Androdon* was placed in the nonhermit subfamily, though bootstrap support for its specific affinities generally was lower than that observed among other hummingbird taxa.

DISCUSSION

Molecular estimates of phylogeny are of particular value for groups in which strong selection has produced superficial resemblances based on shared adaptation, as has undoubtedly occurred many times among hummingbirds (Bleiweiss et al. 1997, Bleiweiss 1999). Cytochrome-*b* sequence data are unequivocal in placing *Ramphodon* with other traditional hermit genera, in demonstrating its sister relationship with an exemplar of the distal and superficially dissimilar hermit *Glaucis*, and in placing the superficially similar *Androdon* in the nonhermit subfamily. Thus, our results reinforce conclusions based on external (Hinkelmann and Schuchmann 1997) and internal (Zusi and Bentz 1982) anatomy that *Ramphodon* is a hermit. However, our data suggest that *Ramphodon* is a more recently diverged member of that clade (compare phylogenetic hypotheses summarized in Fig. 3). Nevertheless, phylogenetic inferences based on infor-

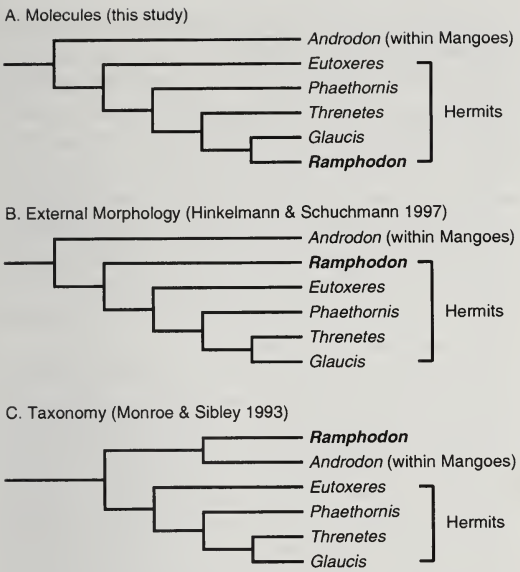

FIG. 3. Comparison of phylogenetic hypotheses proposed for *Ramphodon*. Hypothesis B is based on the study of external morphology by Hinkelmann and Schuchmann (1997). Hypothesis C is based on the placement of *Ramphodon* at beginning of the subfamily Trochilinae (nonhermits) in linear classification of Monroe and Sibley (1993). Compared to log likelihood for heuristic cytochrome-*b* topology A, log likelihoods for alternate (differing from consensus tree in Fig. 2 only in placement of *Ramphodon)* topology B (ln likelihood = −5613.40) or C (ln likelihood = −5635.30) are significantly lower by nonparametric likelihood ratio ($\chi^2_{A\text{-}B} = 40.76$, $\chi^2_{A\text{-}C} = 62.67$; df = 1, two-tailed $P < 0.0001$) and parameteric Kishino-Hasegawa (100,000 RELL bootstrap replicates, two-tailed $P = 0.0012$ for A versus B and $P < 0.0001$ for A versus C) tests (calculated in PAUP*; see also Swofford et al. 1996). Thus, the cytochrome-*b* data strongly favor hypothesis A over either B or C. See text for discussion.

mation from a single mitochondrial gene could be biased because topologs recover only the gene tree rather than the species tree. Here we discuss additional support for our hypothesis, as well as its implications for understanding hummingbird evolution.

Phylogenetic signal.—Relationships among the four traditional hermit genera obtained through analysis of cytochrome-*b* sequences agree in all respects with those indicated by earlier studies based on DNA hybridization (Bleiweiss et al. 1994b, 1997; Fig. 1). Hermits form a basal monophyletic group within hummingbirds. Moreover, *Eutoxeres* defines the first branch within this clade, followed by *Phaethornis* and then *Threnetes-Glaucis*. As DNA hybridization measures genetic divergence over the entire single-copy genome, the congruence between the DNA hybridization-based results and those obtained from our gene sequence study gives us confidence that the topology for hermits, including the additional placement of *Ramphodon*, accurately reflects phylogeny.

For nonhermits as well, cytochrome-*b* data provide support for several relationships inferred from other methodologies, including the pairing of *Colibri* with *Doryfera* (Bleiweiss et al. 1997) and of *Anthracothorax* with *Eulampis* (del Hoyo et al. 1999). Moreover, phylogenies generated from DNA sequencing (herein), DNA hybridization (Bleiweiss et al. 1997), and less strongly, allozymes (Gill and Gerwin 1989, Gerwin and Zink 1998) all suggest that *Androdon* is a nonhermit. However, the specific affinities of *Androdon* differ among (taxa in common between) studies; our sequencing places *Androdon* as a sister taxon to the *Colibri-Doryfera* clade whereas DNA hybridization places *Androdon* as a sister to *Heliothryx* rather than to *Colibri-Doryfera*. For the sequencing data, however, bootstrap values for basal branches among nonhermits in general, and for the *Androdon* node in particular, were low (<50%) in several analyses, thereby echoing lack of resolution suggested by some allozyme studies (Gerwin and Zink 1998). Thus, cytochrome-*b* may better resolve relationships among hermits than among divergent nonhermits. In any case, we consider the specific relationships of *Androdon* within nonhermits unresolved by cytochrome-*b* sequence data.

Character evolution.—The available molecular phylogenies imply that evolution of "toothed" bills in *Ramphodon* and other hummingbirds has both a phylogenetic and homoplastic component (see Fig. 2). The special relationship between *Ramphodon* and *Glaucis* serves to associate the only two hermit taxa known to develop bill serrations, although these serrations are smaller and sometimes develop only on the maxilla in *Glaucis* (*G. dohrnii* sometimes is placed in *Ramphodon*; Monroe and Sibley 1993) as compared to both tomia in male *Ramphodon* (Ornelas 1994). Moreover, males of *Glaucis dohrnii* and of *Ramphodon* also share the unusual hook at the

bill tip lacking in other hermits (Ornelas 1994). Absence of such features in more basal hermits implies that these similarities between *Ramphodon* and *Glaucis* are synapomorphic. Although our sequence data did not provide strong support for placement of *Androdon* within nonhermits, earlier DNA hybridization-based phylogenies indicate that *Androdon* belongs to a second monophyletic group (within the basal Mangoes) whose constituent species are characterized by serrated bills (see discussion in Bleiweiss et al. 1997). Thus, *Ramphodon* and *Androdon* appear to be extreme exemplars within each of two independent radiations of tooth-billed forms.

Hinkelmann and Schuchmann (1997) placed *Ramphodon* and *Eutoxeres* as the two earliest branches, respectively, in hermit phylogeny (Fig. 3B) based in part on their striped underparts, a feature otherwise unusual among hummingbirds (see frontispiece, Fig. 2). However, Hinkelmann and Schuchmann (1997) noted that the striped underparts of *Ramphodon* and *Eutoxeres* might not be "homologous" because the individual feathers differ in detail; those in *Ramphodon* are black along the rachis and have white margins whereas those in *Eutoxeres* are white along the rachis and have black margins. The pattern in *Androdon* is like that in *Eutoxeres* (RB unpubl. data). On the other hand, *Ramphodon* and *Glaucis* share similar facial patterns (dark auricular patch with light trim) and rich ochre head markings (see frontispiece, Fig. 2), features also present in related hermits (*Phaethornis*, *Threnetes*) but absent in other hummingbirds with striped underparts (including *Eutoxeres* within hermits). Thus, striped underparts of *Ramphodon* probably are homoplastic *vis à vis Eutoxeres* and *Androdon*, whereas the distinctive head pattern and color shared by *Ramphodon* and *Glaucis* probably are synapomorphic with such features in other derived hermits.

Despite the striking degree of homoplasy between *Ramphodon* and certain hermits and nonhermits with respect to external morphology, other prominent characteristics of *Ramphodon* appear to concord with its special relationships as defined by molecular data. Thus, the form of the patagial muscle in *Ramphodon* is like that in other derived hermits but unlike that in the basal *Eutoxeres* (Zusi and Bentz 1982, Bleiweiss 2002). Moreover, although all hermits build a conical pendant nest, those constructed by members of the *Threnetes-Glaucis-Ramphodon* clade share thin walls fashioned out of fine roots and fibers, whereas those constructed by the remaining genera have thick walls fashioned out of vegetable matter and detritus (Sick 1993). Additional behavioral and morphological studies will be needed to reveal other ways in which *Ramphodon* is similar to, or divergent from, its putative relatives.

Historical biogeography.—Details about the tempo and mode of *Ramphodon* evolution remain to be determined by future studies that achieve a more detailed sampling of hermit taxa (RB unpubl. data). For example, we sequenced only one species of *Glaucis*, which leaves open the question of whether *Glaucis* as currently defined is monophyletic or paraphyletic with respect to *Ramphodon*. However, the broad outlines of the origin of *Ramphodon* can be gleaned from the results of our study. For example, Stiles (1981) suggested that the hummingbird fauna of southeastern Brazil is relatively old, based in part on the occurrence there of many distinct endemic monotypic forms (e.g., *Stephanoxis*, *Leucochloris*, *Aphantochroa*, *Eupetomena*). Contrary to this hypothesis, the distal placement of *Ramphodon* within hermits suggests that even the most distinctive Brazilian endemics evolved relatively recently (and potentially rapidly). Indeed, *Ramphodon* is younger than the ancestor to the more homogeneous *Glaucis-Threnetes* pairing, which fossil-calibrated DNA hybridization distances date to the Pliocene (approximately 4 mybp; Bleiweiss 1998a).

Previous studies have argued that many species endemic to the lowland forests of southeastern Brazilian evolved there in allopatry after a more widespread ancestor invaded these habitats (Haffer 1974, Willis 1992) including hummingbirds (Bleiweiss 1998b). This hypothesis provides a plausible scenario for the origin of *Ramphodon* because the taxon's closest relatives (*Glaucis*, *Threnetes*) are widespread in the South American lowlands. Thus, the ancestors of *Ramphodon* probably resided in these same habitats. Although we were unable to secure tissues of *Glaucis dohrnii* for analysis, the existence of this second

southeastern Brazil endemic with affinities to *Glaucis* argues that southeastern Brazil was an important locus for *Glaucis* radiation. Without more detailed information about specific interrelationships between *Ramphodon* and members of *Glaucis*, however, it is unclear whether the clade's Brazilian endemics are authocthonous in origin or the result of successive invasions by more widespread forms.

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APPENDIX

Collection localities for specimens used in this study.—Ramphodon naevius: Santa Lúcia field station of the Museu de Biologia Mello Leitão, Santa Teresa, Espirito Santo, Brazil; *Eutoxeres aquila*: Cooperative Salsedo Lindo #1, road from San vicente Maldonado to encampamento de CODESA, 21.6 km from San Vicente Maldonado, Prov. de Pichincha, Ecuador; *Phaethornis yaruqui*: Cooperative Salsedo Lindo #1, road from San Vicente Maldonao to encampamento de CODESA, 21.6 km from San Vicente Maldonado, Prov. de Pichincha, Ecuador; *Threnetes ruckeri*: Centro Científico Río Palenque, 56 km SW Santo Domingo de los Colorados on Río Babo, Prov. de los Ríos, Ecuador; *Glaucis aenea*: below Cooperative Salsedo Lindo #1, road from San Vicente Maldonao to encampamento CODESA, 21.6 km from San Vicente Maldonado, Prov. de Pichincha, Ecuador; *Anthracothorax prevostii*: Central America; *Eulampis holosericeus*: trail to Muskmelon Bay just beyond trail to Crab Cove, Guana Island, British Virgin Islands; *Heliothryx barroti*: Centinella de Guayllabamba, road from San Vicente Maldonado to encampamento de CODESA, 21.6 km from San Vicente Maldonado, Prov. de Pichincha, Ecuador; *Colibri coruscans*: Calle Gonzalo Pizarro, 2.0–2.5 km from Via Interoceania, Barrio Churo Loma, Tumbaco, Prov. de Pichincha, Ecuador; *Doryfera ludovicae*: below Hacnda Santa Rosa on Río Cinto, Prov. de Pichincha, Ecuador; *Androdon aequatorialis*: Cooperative Salsedo Lindo #2, road from San Vicente Maldonao to encampamento de CODESA, 21.6 km from San Vicente Maldonado, Prov. de Pichincha, Ecuador; *Hemiprocne mystacea*: New Guinea; *Streptoprocne zonaris*: old road to Mindo at Y to Mindo, 64.8 km from Ave. Occidental, Prov. de Pichincha, Ecuador; *Chordeiles minor*: Wild Animal Rehabilitation Center, Milwaukee, Wisconsin.

Note: for material from Ecuador, the Caribbean, and the United States, voucher specimens were deposited as study skins, spirit specimens, or skeletons in the collections of the Univ. of Wisconsin Zoological Museum or Museo Ecuatoriano de Ciencias Naturales.

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FIRST NESTING RECORDS OF THE MOUSTACHED ANTPITTA (*GRALLARIA ALLENI*)

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ABSTRACT.—Here we describe the first nesting records of the Moustached Antpitta (*Grallaria alleni*). We found two nests in sub-Andean forests in the Central Andes of Colombia at 1,800 m and in northwestern Ecuador at 1,900 m elevation during November 1995 and March 1999. Both nests were bulky structures with an open deep cup, made with moist plant material, including damp dead leaves, fresh mosses, rootlets, and small stems and fibers. The eggs were aquamarine and the nestlings were covered by dark gray down and had vermilion bills and gapes. Nests of *G. alleni* are similar to the nests of the closely related *G. guatimalensis* in construction and dimensions. This note contributes new information on this endangered and poorly known species. *Received 27 June 2002, accepted 17 December 2002.*

The natural history of *Grallaria* species is poorly known due to their elusive behavior and preference for dense and dark understory (Wiedenfeld 1982, Kattán and Beltrán 1999). To date, nests of only 5 of the 31 existing species have been described, and nothing is known of the breeding biology of 11 species (Fjeldså and Krabbe 1990). Little information on nesting behavior of this genus has been published since the review by Wiedenfield (1982; e.g., see Whitney 1992, Dobbs et al. 2001). Here we present a description of nests, eggs, and nestlings of the Moustached Antpitta (*G. alleni*).

Until recently *G. alleni* was known only from the type of the nominate subspecies and the type of *G. a. andaquiensis* (Hernández and Rodríguez 1979). It was recently rediscovered in Colombia (Renjifo 1999), and recorded for the first time in Ecuador (Krabbe and Coopmans 2000). The currently known distribution of this species includes both slopes of the Central Andes and the upper Magdalena Valley in Colombia, between 1,800 and 2,135 m elevation, and both slopes of the Andes in northern Ecuador, between 1,800 and 2,500 m (Krabbe and Coopmans 2000, Renjifo 2002, JFF unpubl. data). This species is considered endangered due to habitat destruction (BirdLife International 2000, Freile 2002, Renjifo 2002).

On 23 November 1995, LMR found a nest with a recently hatched nestling and an egg in the Santuario de Flora y Fauna Otún-Quimbaya (04° 43′ N, 75° 35′ W), Risaralda Dept., at 1,800 m elevation, on the western slope of the Central Andes of Colombia. The nest was located in a small, flat valley surrounded by steep slopes inside secondary forest with canopy height approximately 13 m. The area was very close to old growth forest and to forest edge along an abandoned pasture, and just a few meters from a creek.

The nest was built within a hanging tangle of the epiphyte *Philodendron astatum* (Araceae) and to a lesser extent *Columnea* sp. (Gesneriaceae). The nest was a bulky, roughly spherical structure truncated at the top. It contained a deep cup lined with stiff plant fibers (mainly rootlets). It was constructed primarily of dead parts of *P. astatum* with small stems and leaves of other plants. Upper parts of the nest, including the sides of the cup, were lined with damp dead leaves of *P. astatum*, forming a compact structure (Fig. 1). It had an external diameter of 23 cm and an external height of 17.0 cm. The cup was 10.0 cm in diameter and 7.0 cm deep.

The nest was located 130 cm above the forest floor, supported by hanging stems of *P. astatum* and branches of a small shrub, close to the trunk of a small tree that supported the tangle of epiphytes, but not in contact with it. Owing to its shape, location, and construction material, the nest was well concealed and was very difficult to detect in the dark understory.

The egg was unmarked aquamarine and

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FIG. 1. Nest of Moustached Antpitta (*Grallaria alleni*) in dense understory vegetation. Santuario de Fauna Otún-Quimbaya, Risaralda, Colombia, 23 November 1995 (photograph by L. M. Renjifo).

measured 30.7 mm × 24.7 mm. The day after the nest was found the second egg had hatched. The nestlings had closed eyes, dark gray skin covered with dark gray down, and a prominent vitelline sac. The bill (except for a dark tip) and the gape were vermilion. Nestlings hid their heads under their own bodies when handled, as though to conceal the brightly colored bills. Two days after hatching, the nestlings weighed 12.0 and 13.5 g. Body measurements (in mm) were: culmen 8.0 and 9.3, tarsi 13.6 and 14.8, and wing 12.0 and 12.0, respectively.

At the time the nest was found an adult was on it. A few days later the adult was again observed sitting in the nest, with its head, neck, and upper mantle visible. Seven days after the second egg had hatched (5 December) the nest was found empty and tilted, suggesting that it had been preyed upon. Subsequently, the nest was collected and deposited at the Inst. de Ciencias Naturales of the Univ. Nacional de Colombia (ICN N-105). It belongs to the nominate subspecies *G. alleni alleni*. Otún-Quimbaya is <15 km north of the type locality; one specimen of this subspecies was collected by M. J. Braun on 30 May 1999 just a few hundred meters from the place where this nest was located, and deposited at Inst. Alexander von Humboldt (IAvH 10741).

On 8 March 1999 JFF found a nest of *G. alleni andaquiensis* with two nestlings at Bosque Integral Otonga, Cotopaxi Province, northwestern Ecuador (00° 25′ S, 79° 00′ W), at 1,900 m elevation. The nest was located in a wet secondary forest on a gentle slope. This forest had a fairly open understory (15–20% coverage), with shrubs, some moss-covered vines and epiphytes. The nest was 90 cm away from a frequently used path inside the forest.

The nest was a bulky structure with an open and deep rounded cup. It had a compact texture on the surface (Fig. 2). This nest was constructed primarily of leaf litter and rootlets, with a few dead sticks in the base. Externally, it was covered with plant fibers, rootlets and abundant live wet mosses, making it very dif-

FIG. 2. Nest of Moustached Antpitta (*Grallaria alleni*) with two nestlings 4–5 days old. Bosque Integral Otonga, Cotopaxi, Ecuador, 8 March 1999 (photograph by J. A. Chaves).

ficult to detect. On one side the nest had a small protruding platform made of densely woven, damp, dead leaves. The nest was built over a *Bohemeria* sp. (Urticaceae), a second growth shrub. It was supported by a mossy diagonal branch, and was covered by three other diagonal to almost vertical branches, 135 cm above the forest floor. It had an external diameter of 22.0 cm and an external height of 22.5 cm. The cup was 11.8 cm in diameter and 4.5 cm deep.

The nestlings were covered in dark gray down. They had feather sheaths on the wings, and a bright orange gape and mouth (Fig. 2). Judging from the descriptions given by Miller (1963) and Dobbs et al. (2001) for *G. guatimalensis*, these nestlings probably were 4–5 days old (i.e., closed eyes, slight development of wing feathers, begging behavior).

JFF observed two adult birds attending the nest and feeding the nestlings. The adults captured arthropods on the ground on trails

and forest floor. After feeding the nestlings, the adults usually remained motionless for several minutes on the protruding platform with their backs facing out, which completely concealed the nest entrance. There was very little vocal activity in the area. The nest was empty a week later (T. de Vries pers. comm.), suggesting that it probably had been depredated.

The nest at Otún-Quimbaya was found during the second rainy period of the year, and a juvenile was observed by LMR at the same locality on 5 July 1996 (at the beginning of the first dry season of the year). The nest at Otonga was found at the peak of the rainy season. These three records might suggest that the breeding season of the species coincides with rainy seasons.

Both nests described here were similar in construction and dimensions to the nests of *G. guatimalensis*, which is considered a closely related species (Hernández and Rodríguez 1979, Krabbe and Coopmans 2000). Nests of *G. alleni* tend to be bigger than those of *G. guatimalensis*, although with an overlapping range of measurements for: external height (mean = 14.5 cm ± 4.7 SD, n = 10), cup depth (mean = 4.8 cm ± 1.5 SD, n = 10), internal cup diameter (mean = 9.9 cm ± 0.97 SD, n = 8), as well as height above forest floor (mean = 102.7 cm ± 37.9 SD, n = 9). Nests of *G. alleni* were bigger than those of *G. guatimalensis* for external diameter (mean = 17.3 cm ± 3.4 SD, n = 10; data from Edwards and Lea 1955, Miller 1963, Rowley 1966, Dobbs et al. 2001, F. G. Stiles pers. comm.). Nests of both species also were similar in terms of building material, shape, disposition, and habitat. Nests of *G. alleni* were built on branches or within tangles close to the trunks of small trees, consistent with most nests of *G. guatimalensis* reported in the literature (Dobbs et al. 2001, but see Edwards and Lea 1955, Miller 1963, Rowley 1966). One of the nests of *G. alleni* had abundant green mosses on the external surface, a feature that is shared with the nests of *G. guatimalensis* described by Dobbs et al. (2001). Habitat characteristics of the two *G. alleni* nests were similar to the nests of other *Grallaria* species, and are congruent with most previous nesting reports of the genus in terms of clutch size, color pattern of eggs, and coloration of nestlings (Wiedenfeld 1982, Quintela 1987, Whitney 1992, Protomastro 2000).

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NEST SITE CHARACTERISTICS OF AMERICAN ROBINS BREEDING IN DESERT-RIPARIAN HABITAT

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ABSTRACT.—We describe the nest site characteristics, and report on the association between site characteristics and reproductive success (brood size at day 8), for a population of American Robins (*Turdus migratorius*) breeding in the Toiyabe Mountains of central Nevada. Based on data from 132 nests, the immediate vicinity (a 10-m radius) around robin nests was sparsely vegetated with limited cover at any vegetation height. Nest tree diameters at breast height were not significantly different from those of nearby trees. Based on tree availability in the immediate vicinity, robins chose to nest in single-leaf pinyon (*Pinus monophylla*) more often (49.6% of nests used versus 39.3% availability), and quaking aspen (*Populus tremuloides*) less often (24.8% of nests used versus 52.1% availability), than expected by chance. Contrary to predictions based on previous studies, there was no change from coniferous to deciduous trees for nesting as the breeding season progressed, nor did robins build their nests higher in trees later in the season. Nest orientation was significantly directional in the 90° arc between east and south, but was unrelated to the amount of concealment conferred by shrub and bush cover in the four quadrants around the nest. Solar insolation resulting from nest placement was not related to brood size at day 8 and there were no discernable relationships between either solar insolation or orientation and clutch initiation date. Brood size on day 8 was inversely related to mean dbh of the surrounding trees, while canopy cover and height were associated positively with larger broods at day 8. *Received 13 February 2002, accepted 20 February 2003.*

Although researchers often know a great deal about the basic biology of endangered species, it is not unusual for similar information to be lacking for common species. The American Robin (*Turdus migratorius*) is a widespread North American species that is a habitat generalist, occupying residential areas, woodlands, open forests, as well as early through late seral forest, and showing broad acceptance of a variety of overstory species (Tyler 1949, Sallabanks and James 1999). Recent research has elucidated the diet, foraging ecology, and geographical variation in morphology and appearance of the robin (e.g., Wheelwright 1986, Aldrich and James 1991, Jung 1992, Sallabanks 1993). However, studies of this species' nesting habits and nest site characteristics have been limited, and often focused on human-altered landscapes such as agricultural settings, tree plantations, and urban areas (e.g., Howell 1942, Young 1955, Savard and Falls 1981, Yahner 1982, Hughes and Hudson 1997). Data on nest tree characteristics and nest placement presented in the review of the American Robin by Sallabanks and James (1999) were based on unpublished data with no comparisons made to the trees or placement opportunities that were available in the surrounding habitat.

Nest placement patterns, and any seasonal changes in those patterns, may be interpreted in the context of the relationship between selection of nest site characteristics and the risk of predation (e.g., Stauffer and Best 1986, Marzluff 1988, Möller 1988). For instance, American Robins exhibited seasonal changes in nest height (higher later in the breeding season; Howell 1942) and tree type selected for nest substrate (coniferous trees early in the season, deciduous trees later; Howell 1942, Savard and Falls 1981). These adjustments may be related to deterring predators in a changing environment. Likewise, Davidson and Knight (2001) suggested that within the relatively open landscape in which robins nest, placement of a nest in dense understory vegetation at a habitat edge might provide better cover than would interior forest locations. This presumed that nest depredation from visually oriented predators was an important selective factor. In the congeneric Eurasian

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Blackbird (*Turdus merula*), habitat structure was a significant predictor of nesting success during egg laying and incubation, when concealment may have prevented nest discovery, but not after eggs hatched and auditory cues became more important to predators (Hatchwell et al. 1996).

Our goal was to describe the nest site characteristics of American Robins breeding in a desert-riparian community. Our specific objectives were to (1) examine nest placement relative to the vegetation available immediately adjacent (within 10 m) to the nest, (2) look for changes in nest placement associated with seasonal changes in physiognomy, and (3) assess the potential association among local vegetation characteristics (microhabitat within 10 m of the nest), solar insolation, and the number of young present at day 8 of the nestling phase.

METHODS

We collected data during the summers of 1995–1996 in central Nevada. We searched for nests in canyons along five permanent streams (San Juan, Stewart, Clear, Marysville, and Washington Creek) on the western side of the Toiyabe Mountain Range (39° 30′ N, 117° 05′ W). Canyon floors typically are narrow with 4- to 50-m wide riparian zones dominated by stands of quaking aspen (*Populus tremuloides*) interspersed with willows (*Salix* spp.) and water birch (*Betula occidentalis*), along with grassy meadows densely populated by *Carex* spp., *Poa* spp., *Juncus* spp., and *Deschampsia* spp. (Weixelman et al. 1996). Canyon slopes adjacent to these riparian zones are steep, rocky and characterized by low density upland forests consisting largely of single-leaf pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*), with an understory of sagebrush (*Artemisia* spp.; Weixelman et al. 1996). These canyons were subject to varying levels of livestock grazing and use as recreational areas prior to and during the study, as well as natural disturbances, all of which altered the habitat to varying degrees (Weixelman et al. 1996).

We searched suitable habitat in all drainages beginning on 1 June 1995 and 1 May 1996 and continued until mid July of both years. During 1995, in addition to active nests we also searched for previously constructed robin nests that had sufficient structure remaining to be positively identified. These additional nests are referred to hereafter as 1994 nests, although some may have been older and others may have been early 1995 nesting season failures. We monitored active nests every 3–4 days from discovery to the end of day 8 (first egg hatched on day 0) of the nestling phase, or until the nest failed. We determined the clutch initiation date, final clutch size, and number of young present at day 8 of the nestling phase for all nests. Day 8 was chosen for determining nesting success to avoid the potential premature fledging of young caused by such visits, and to limit the attraction of nest predators, particularly *Corvids*. Although most nest failures occur at the egg rather than nestling stage (Kendeigh 1942), as a consequence of our methodology we likely missed the loss to predators of some nestlings that occurred between day 8 and the normal date of fledging for this species on day 13 (Sallabanks and James 1999). Thus we may have overestimated the number of young produced from nests associated with certain characteristics. When we discovered nests after clutch completion or hatching, we estimated the age of the chicks based on an aging key we developed using the morphological characteristics of known-age chicks from seven nests (see Appendix). For these nests, we determined clutch initiation date based on a 13-day incubation period (Howell 1942, Young 1955). For any nests found after day 8, we assumed that the number of nestlings present on discovery had been present on day 8. Although we saw Brown-headed Cowbirds (*Molothrus ater*) on our study site, we found no evidence of cowbird parasitism in any robin nests. Our protocol did not allow us to distinguish between nest failures caused by adult abandonment due to predation, starvation, or cold weather and those due to predation of eggs or chicks. However, none of our data on chick mass (i.e., growth rates) suggested that chicks in a particular nest starved to death resulting in nest failure.

During 1995, we collected data on nest site characteristics for all 1994 and 1995 nests. For each nest, we recorded the species of tree in which the nest was placed, diameter at breast height (dbh) of the nest tree, height of

the nest, direction the nest faced relative to the center of the tree (unlike for nest cavity openings, determining this bearing for a nest cup was somewhat subjective and so we measured orientation to the nearest 45°; i.e., N, NE, E, SE, etc.), and distance to the nearest body of water. To characterize the habitat in the 10-m radius area surrounding each nest tree, we examined 12 variables in four quadrants (NE, NW, SE, and SW) around each tree. We measured distance to the nearest tree (dbh <10 cm) in each quadrant and recorded its dbh and species. Other types of woody vegetation fell into two categories: shrubs (multistemmed at base and height >1 m) and bushes (multistemmed but <1 m tall). For each quadrant we recorded the distance from the nest tree to the nearest shrub and nearest bush. For the purposes of data analyses, when there was no tree, shrub, or bush within 10 m, we entered this into the database as a missing value for distance. For each 10-m radius area, we estimated mean canopy height to the nearest 0.5 m in each quadrant using a Suunto optical reading clinometer, and we visually estimated the percent foliage cover to the nearest 5% for each canopy layer (tree, shrub, and bush), as well as for the extent of grass-forb ground cover and bare ground. We developed an index of overall vegetation density (value reflects percentage of sky blocked by vegetation) using a spherical densiometer held at elbow height in the middle of each quadrant. Except where noted, for statistical purposes we calculated mean values from the four quadrants for dbh of the nearest tree, distance to the nearest tree, distance to the nearest shrub, distance to the nearest bush, mean canopy height, percent canopy cover, percent shrub cover, percent bush cover, percent grass-forb ground cover, percent bare ground cover, and vegetation density. For nests found during 1996, we recorded data for orientation, height of the nest, and nest tree species, but no other vegetation variables due to logistical constraints.

We estimated solar insolation using the Arc Macro Language program Solarflux (Hetrick et al. 1993) for nest locations from 1995 and 1996 plotted on 1:50,000 scale topographic maps. Based on a 30-m horizontal resolution digital elevation model provided by R. Connell of the Toiyabe National Forest, we completed these calculations using the Arc/Info Grid Module. Variables estimated for each nest included total amount of solar radiation (kJ) incident on the nest tree's location for 1 May and 21 June, as well as the number of hours of direct sunlight expected with clear skies on those two days. These values incorporated the effects of topography around the nest, but did not account for the potential impact of local shading by adjacent vegetation.

Statistical analyses.—Because we did not collect data for all variables for each year of the study, sample sizes varied by analysis. To examine nest placement relative to the vegetation available in the immediate vicinity, we used paired *t*-tests to compare the dbh of the nest tree with the mean dbh of the nearest trees from all four quadrants. We also examined the choice of nest tree species at this localized scale by comparing the frequency of species chosen with the frequency of species detected as the nearest tree in the four quadrants for all nests. Using a *G*-test (Zar 1996), we evaluated choice after eliminating three species that had been used as nests but had not been identified among species of nearest tree in a quadrant for any nest. Those species eliminated included water birch (two nests), black cottonwood (*Populus balsamifera*; three nests) and willow (*Salix* spp.; eight nests).

The cover provided by nearby vegetation may have influenced nest placement through its effects on concealment of the nest and access to escape routes for attending adults (cf. Wiebe and Martin 1998). We used a two-tailed binomial test (Zar 1996) to assess the probability that the quadrant toward which the nest pointed had either the most dense vegetation (reflected through having the smallest distance to the near tree, the highest shrub cover, or the highest bush cover among the four quadrants), or the least dense vegetation (greatest distance to the near tree, the lowest shrub cover, or the lowest bush cover).

To test the hypothesis that robins changed the nest tree species they used over the season (Howell 1942, Savard and Falls 1981), we divided the nesting season into 15-day periods and compared the proportion of conifer nest trees (single-leaf pinyon or Utah juniper versus all other species) used from 1 May through 30 June using a *G*-test. We used a simple linear regression of nest height on

TABLE 1. Nest and local vegetation characteristics within 10 m of the nest for American Robins breeding in riparian habitat of central Nevada, 1994–1996.

Variable	Mean ± SD	*n*
Nest height (m)	2.3 ± 1.2	116
Nest tree dbh (cm)	18.5 ± 9.0	62
Dbh of the nearest tree (cm)[a]	19.7 ± 6.8	66
Distance to the nearest tree (m)[a]	6.3 ± 2.3	70
Distance to the nearest shrub (m)[a]	4.6 ± 2.8	70
Distance to the nearest bush (m)[a]	2.1 ± 1.5	70
Height of the canopy (m)[a]	6.7 ± 3.5	70
Percent canopy cover[a]	12.2 ± 8.3	70
Percent shrub cover[a]	11.4 ± 9.8	70
Percent bush cover[a]	11.4 ± 8.6	70
Percent grass-forb ground cover[a]	27.1 ± 15.2	70
Percent bare ground[a]	41.4 ± 20.9	70
Vegetation density[a]	63.0 ± 21.7	70
Distance to water (m)	19.3 ± 17.3	70

[a] Mean values for the four quadrants around the nest tree (missing values were ignored).

clutch initiation date to test the hypothesis of Howell (1942) that early breeding American Robins nested lower in trees than those nesting later.

Related to our examination of potential links between solar insolation or local vegetation and brood size at day 8, we analyzed orientation data using a Rayleigh test to determine the statistical significance of the mean angle for nests in each canyon (Zar 1996). For this analysis, we converted orientations (N, NE, E, . . .) to their 45° equivalents, analyzed the data, and then converted the resulting values back to the nearest orientation designation (N, NE, E, . . .) for presentation. Multivariate examination of vegetation characteristics versus clutch size, brood size at day 8, and brood loss included data from 1995 nests. We assessed the possible relationship between the solar insolation variables, nest orientation, estimated clutch initiation date, and our measures of productivity (clutch size, brood size at day 8, and partial brood loss which was represented as brood size/clutch size). We used a backward stepwise multiple regression to conduct the latter analysis. Similarly, we examined the association between local vegetation characteristics and our measures of productivity (clutch size, brood size at day 8, and brood loss) with the same technique. We used SAS version 8.12 (SAS Institute, Inc. 2001) for all statistical analyses; dependent variables were rank transformed for those data not normally distributed (Conover and Iman 1981). We considered relationships to be statistically significant when $P < 0.05$.

RESULTS

We found 132 American Robin nests in the five canyons, 42 from 1994, 28 in 1995, and 62 in 1996. The immediate vicinity around these nests was vegetated sparsely with trees, bushes, and shrubs, and there was limited cover at any canopy layer (Table 1). There were extensive amounts of bare ground around the nest trees and nests were substantial distances from the nearest water, given that most riparian strips were less than 50 m wide. Vegetation in the quadrant toward which the nest faced was neither the most nor least dense around the nest, based on distance to the nearest tree or percent cover by shrubs or bushes (*P* values for the six comparisons ranged from 0.13 to 0.76).

We found no significant difference between the dbh of nest trees and the mean dbh of the nearest trees in each of the four quadrants when all species were combined ($t = 0.83$, df = 60, $P = 0.41$; power = 100%). This pattern held also within species when we compared the dbh of aspen and pinyon nest trees with the mean dbh of the nearest conspecific trees around them (respectively, $t = 0.89$, df = 18, $P = 0.38$, power = 100%; $t = 0.79$, df = 31, $P = 0.44$; power = 100%; Table 2). Based on comparison with the percent availability of adjacent trees in the immediate vicinity of the nest (Table 2), American Robins used quaking

TABLE 2. American Robins breeding in riparian habitat of central Nevada, 1994–1996, used nest trees with a species composition significantly different from that available within 10 m of the nest tree (percentage reported with actual number in parentheses). Mean dbh for quaking aspen and single-leaf pinyon nest trees and the nearest adjacent conspecific were not significantly different.

Species	Used	Mean dbh ± SD (*n*)	Available	Mean dbh ± SD (*n*)[a]
Aspen	24.8 (31)	23.5 ± 10.8 (18)	52.1 (110)	20.6 ± 8.0 (18)
Birch	1.6 (2)		0	
Cottonwood	2.4 (3)		0	
Juniper	9.6 (12)		5.2 (11)	
Mountain Mahogany	5.6 (7)		3.3 (7)	
Pinyon	49.6 (62)	16.5 ± 7.3 (31)	39.3 (83)	18.7 ± 5.6 (31)
Willow	6.4 (8)		0	

[a] Mean values for the conspecific nearest the nest tree within each of four quadrants around the nest tree.

aspen less frequently (24.8% of 125 nests) than expected and put their nests in single-leaf pinyon (49.6% of 125) more often than expected by chance ($G = 19.191$, df = 3, $P < 0.0001$). However, there was no significant change in the proportion of nests placed in conifers as the nesting season progressed from the beginning of May through the end of June ($G = 0.791$, df = 3, $P = 0.85$). We found a significantly positive relationship between nest height and clutch initiation date, but initiation date explained very little of the variance in nest height ($r^2 = 0.08$, $F_{1,69} = 5.77$, $P = 0.019$). Mean first egg date was 27 May (SD = 18 days, $n = 80$).

The mean angle of orientation for nests in each of the canyons indicated a tendency for the nest to face within the 90° arc between east and south (Table 3). However, only the data from San Juan Creek canyon, and all canyons combined, had a statistically significant vector. Although statistically significant in two cases, none of our incident solar insolation variables, nor orientation or clutch initiation date, explained biologically meaningful amounts of the variation in clutch size ($r^2 = 0.06$, $F_{1,56} = 3.78$, $P = 0.06$; reduced model included only orientation), brood size at day 8 ($r^2 = 0.06$, $F_{1,76} = 4.43$, $P = 0.039$; reduced model included only solar insolation on 21 June), or partial brood loss ($r^2 = 0.08$, $F_{1,59} = 4.94$, $P = 0.030$; reduced model included only solar insolation on 21 June). Likewise, clutch initiation date was not significantly correlated with either solar insolation on 1 May or hours of direct sunlight on 1 May (Pearson correlation coefficients; $r = 0.18$, $n = 80$, $P = 0.11$, and $r = 0.16$, $n = 80$, $P = 0.13$, respectively).

TABLE 3. Orientation with respect to the tree trunk for the nests of American Robins breeding in the riparian habitat of five canyons in central Nevada, 1994–1996. There is a strong east to south tendency.

Canyon	Orientation	*n*	*Z*	*P*
San Juan	S	38	5.66	0.003
Clear	SE	33	2.38	0.093
Stewart	E	32	2.91	0.054
Washington	SE	6	0.25	0.829
Marysville	E	14	1.52	0.233
Combined	S	123	3.48	0.033

We had insufficient data to examine the relationship of vegetation with clutch size or brood loss (data available on clutch size for only 14 nests from four canyons in 1995 when necessary vegetation data was collected). However, examination of the data on brood size at day 8 and vegetation variables indicated that mean dbh of the nearest trees, mean canopy cover, and mean canopy height were useful predictors, along with nest tree species, of brood size ($r^2 = 0.53$, $F_{6,16} = 3.05$, $P = 0.034$). Pearson correlation coefficients were negative for the three numerical variables, suggesting that brood size was higher where mean dbh of trees in the surrounding area was small, and both canopy height and canopy cover were low. Posthoc tests (PROC GLM; SAS Institute, Inc. 2001) for differences among nest tree types in day 8 brood sizes, however, were unable to distinguish the tree species involved for either this restricted database from 1995, or for a larger database of 80 nests from 1995 and 1996 for which we

recorded both reproductive data and nest tree species.

DISCUSSION

The American Robin is an open country or edge species that often does well in suburban or modified rural habitats (Sallabanks and James 1999). Our results indicate that they also used relatively open habitat in desert-riparian communities. In qualitative comparison with the data presented by Sallabanks and James (1999) for robins breeding in Idaho, Washington, Oregon, and Montana, robins in our study population nested lower in trees and used trees with greater dbh. In addition, robins nesting in the Toiyabe Mountains of central Nevada occurred in forest stands with canopy covers that were lower than those of nest sites in the Pacific Northwest. Single-leaf pinyon and quaking aspen were the two most commonly chosen nest trees, but unlike the results reported by Howell (1942) for Ithaca, New York, and Savard and Falls (1981) for Toronto, Ontario, we found no seasonal shift in the tendency to use conifers, nor did we find as Howell (1942), despite a statistically significant relationship, a biologically meaningful association between the date of clutch initiation and nest height.

Contrary to the findings of Sallabanks and James (1999), American Robins in this population placed their nests at a particular orientation with respect to the center of the tree. Our study area was desert-riparian habitat, and the mean elevation for the 1995 and 1996 nests was 2,319 m ± 141 SD. Consequently, our observation of nest orientation from south to east suggests positioning to take advantage of early morning to midday heating after cool mountain nights, followed by shading in the afternoon during higher temperatures. This is consistent with arguments proposed for both New World (Balda and Bateman 1972) and Old World (MacLean 1976) desert-breeding species. Such thermoregulatory-based positioning also concurs with cavity orientation by Red-naped Sapsuckers (*Sphyrapicus nuchalis*) breeding in the same study area (Butcher et al. 2002). Previous studies of open cup-nesting species revealed a westward orientation for some (e.g., Hermit Thrush, *Catharus guttatus*, with a southward to westward tendency; Martin and Roper 1988) and others that were less clear, with bimodal northward or southward orientations (e.g., Western Kingbirds, *Tyrannus verticalis*; Bergin 1991). However, although our nest orientation data suggests use of sites by American Robins with more exposure to the sun early in the day, we could not link this pattern to any of our measures of solar insolation. Likewise, there were no measurable associations among solar insolation, orientation, and clutch initiation date or brood size at day 8. Our analyses of tree density (as reflected in distance to the nearest tree) and vegetation cover at low to midcanopy levels (as reflected in percent shrub cover and percent bush cover) suggests that robins did not orient their nests in the tree toward either the most densely or sparsely vegetated quadrant immediately adjacent to the nest. This pattern was consistent with the finding of Wiebe and Martin (1998) that nest sites with intermediate levels of cover were sought out because they provided some concealment but allowed both the surroundings to be surveyed for predators, as well as a route for escape.

Productivity, as we measured it, appeared be associated with the degree of openness of the canopy. The negative correlations among three variables related to the size and density of trees and brood size at day 8 indicates that robins nesting in open or edge habitat with a low and sparse canopy were more productive than were those nesting in areas with larger trees and greater canopy cover. However, variables related to the density or cover of either shrubs or bushes were absent from the regression. This result indicates that, at least for our study population, Davidson and Knight's (2001) hypothesis that edge effects related to shrub cover positively influence American Robin productivity is not supported. Results from studies of other species on the links between nest concealment and predation rates are contradictory and experimental studies suggest that nest concealment was not a factor in egg or nestling predation (Howlett and Stutchbury 1996). The absence of an association between brood size at day 8 and nest-concealing understory vegetation supports the idea that concealment, as we measured it, is a weak determinant of nesting success. Our results also differ from those of Hatchwell et al. (1996) in that we were able to identify features of the vegetation around the nest that

were useful in predicting the success during brood rearing, whereas Hatchwell et al. (1996) found such information useful only during the egg-laying and incubation periods.

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APPENDIX

Ageing characteristics for American Robin chicks; Day 0 equals hatch day. Naming of feather tracts follows Welty (1979) except for the use of alula, primary, and secondary that follows Pyle et al. (1987). Development of feather sheaths was divided into four stages: (1) discoloration of feather tracts visible below skin, (2) feather sheaths visible under skin and causing skin surface to appear raised, (3) feather sheaths emerge from tract area but are not free of the skin, and (4) emergence of feather sheaths from the skin. Eyes were closed if they could not be opened by gently pulling the skin above them, partially open when nestlings could voluntarily hold eyelids open far enough for the eye to be visible, and open when the nestling could voluntarily hold its eyes open as adult birds do.

Age	Diagnostic characteristics
Day 0	The capital region has two long tufts of down above the eyes and four tufts above the nape. The caudal tracts have tufts of down where each retrix will eventually emerge, the humeral area is covered with down, tufts of down are present where the secondaries will emerge, and the spinal area is covered by a single stripe of down.
Day 1	Light ridges appear on the skin of the breast and belly where the ventral feather tract discoloration will appear on day two.
Day 2	The capital, ventral, spinal, humeral, alula, primary, and secondary feather tracts become discolored. Discoloration appears as tiny gray to black dots. Discoloration of the secondary tracts is lighter than that of the primary tracts.
Day 3	Feather tract discoloration of the ventral, spinal, and humeral areas changes from individual dots to solid areas of discoloration. Primary and secondary feather sheaths become visible under the skin as heavy ridges on the trailing edge of the wing. The first discoloration of caudal feather tracts appears.
Day 4	Nestling eyelids can be separated by gently stretching the skin above them upward. The alula feather sheaths become visible under the protuberance of skin on the leading edge of the wing. Primary and secondary feather sheaths extend from the trailing edge of the wing, but not from the skin, giving the trailing edge a serrated appearance.
Day 5	The nestling can hold its eyes partially open while handled. Feather sheaths become visible under the skin on the capital, ventral, spinal, and humeral regions. The alula feather sheath protrudes from the leading edge of the wing but is still covered by skin. Primary feather shafts emerge from the skin. Caudal tract feather sheaths become visible under the skin.
Day 6	Sheaths of the capital, ventral, spinal, humeral, alula, and secondary feathers emerge from the skin.
Day 7	The nestling can hold its eyes completely open and the caudal tract feather sheaths emerge from the skin.
Day 8	Day 8 nestlings are distinguishable from day 7 nestlings by the extent to which their feathers have broken from their sheath coverings. The ventral, humeral, and spinal areas are well feathered but the alula, caudal, and secondary feathers are still enclosed in their sheaths. Just the tips of the primary feathers are free from their sheaths. Nestlings also become very good at jumping, but still crouch down when returned to the nest, unlike their day 9 and day 10 siblings who try to leap out when returned.

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NEST SITE CHARACTERISTICS IN THE SONG SPARROW AND PARASITISM BY BROWN-HEADED COWBIRDS

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ABSTRACT.—We studied populations of Song Sparrows (*Melospiza melodia*) on 11 islands near Victoria, British Columbia, to evaluate the relationship between nest site characteristics and parasitism by Brown-headed Cowbirds (*Molothrus ater*). For all nests we recorded their height, the height of vegetation above the nest, the percentage of overhead and side exposure, the number of perches in trees and shrubs within 10 m of the nest, and the distance to the nearest tree or shrub perch. Song Sparrow nests within 10 m of trees were parasitized more often than those farther from trees. Estimates of overhead and side exposure also were lower for parasitized nests than unparasitized nests. Our results support the hypotheses that the proximity of trees, and the amount of concealing cover around host nests, influence the success of cowbirds searching for nests to parasitize. *Received 14 June 2002, accepted 14 December 2002.*

Song Sparrows (*Melospiza melodia*) are among the most common hosts of the Brown-headed Cowbird (*Molothrus ater*; Lowther 1993, Scott and Lemon 1996), and suffer higher nest failure and a lower net reproductive rate when cowbirds are abundant (Arcese et al. 1992, 1996; Smith and Arcese 1994; Arcese and Smith 1999; Smith et al. 2002). Because the reproductive success of Song Sparrows may depend upon their ability to evade detection by cowbirds, we investigated the role of vegetation structures near the nest as potential factors affecting cowbird parasitism.

Hauber and Russo (2000) listed four main hypotheses of cowbird nest-searching behavior, of which we consider two. The Nest Exposure Hypothesis predicts that relatively exposed nests are most likely to be parasitized. Some support for this hypothesis exists (Larison et al. 1998, Moskát and Honza 2000), but other studies found no relationship between vegetative cover and parasitism, or found that the relationship between cover and parasitism varied by study site (Clotfelter 1998, Howe and Knopf 2000, Hauber and Russo 2000). Moskát and Honza (2000) showed that nest exposure and the distance to a suitable perch each were related to the probability of parasitism by Common Cuckoos (*Cuculus canorus*), but suggested that perch proximity was the most influential of these variables.

The Perch Proximity Hypothesis suggests that the ability of cowbirds to locate nests is enhanced when perches are available from which to survey the nesting area. In support of this hypothesis, Hauber and Russo (2000) showed that perch proximity was a positive predictor of the frequency of parasitism by Brown-headed Cowbirds of Song Sparrows. Researchers studying other cowbird hosts have reported similar relationships (e.g., Freeman et al. 1990, Clotfelter 1998).

We studied cowbird parasitism of Song Sparrows on 11 small islands located about 20 km northeast of Victoria, British Columbia, Canada. Our goal was to test if one or more of several variables associated with nest concealment and the proximity of trees or perches in shrubs were related to the frequency of parasitism by cowbirds. We predicted that nests with more overhead and side cover, and fewer perches and trees within 10 m, would be parasitized less often than other nests. We also discuss briefly some implications of our results in the context of our long term study of cowbird parasitism of Song Sparrows on Mandarte Island, British Columbia.

METHODS

Study area.—We attempted to monitor all Song Sparrow nests initiated on 11 islands (centered approximately 48° 38′ N, 123° 17′ W) from April through July, 2001. The 11 islands were Mandarte (8.1 ha), Kerr (2.9 ha), Rubly (2.9 ha), Little Shell (0.6 ha), Reay (0.5

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ha), Dock 1 (0.5 ha), Dock 2 (0.4 ha), Dock 3 (0.2 ha), Strawberry (0.2 ha), Imrie (0.2 ha), and Sidney Spit (0.4 ha). Nesting habitat varied slightly among islands, but most nests occurred in blackberry (*Rubus ursinus* and *R. macrocarpum*), rose (*Rosa nutkana*), snowberry (*Symphoricarpos albus*), or other herbaceous vegetation and grasses. The islands vary in their proximity to other islands and the amount of forest cover. Mandarte Island supports a large colony of Glaucous-winged Gulls (*Larus glaucescens*) and has only a few small, live trees within shrub patches. Kerr and Rubly islands support mature Douglas Fir (*Pseudotsuga menziesii*) forests. Little Shell, Reay, and Dock 1 and 2 have a mix of meadow habitat with several moderately sized trees. Dock 3, Strawberry, Imrie, and Sidney Spit have no trees.

Data collection.—We banded all Song Sparrows with a USFWS band and a unique combination of three colored plastic bands. We visited the territories of all birds every 2–5 days to locate all active nests and record nest contents, nest failure, and parasitism by cowbirds. We found the majority of nests during incubation, and attempted to visit nests only when potential predators or brood parasites were not in view.

After young fledged or nests failed, we placed a 6.5-cm diameter orange ball in the nest cup to estimate the visibility of nests from overhead and side positions, each to the nearest 5%. To estimate "side exposure" we recorded the percentage of the top half of the ball that was visible to a human observer positioned at nest height, at a distance of 1 m, in each of the four cardinal directions. We then summed these records and divided by four to obtain a mean estimate of side exposure from 0 to 100%. We estimated "overhead exposure" as the percentage of the ball visible from 1 m directly above the nest.

We measured nest height to the nearest 1 cm from the ground to the rim of the nest cup, and measured vegetation canopy height to the nearest 1 cm from the ground to the approximate edge of the canopy directly above the nest. We counted the number of perches in shrubs and the number of trees within 10 m of the nest, where trees were defined as live or dead woody vegetation >3 m in height. We defined shrub perches as live or dead branches extending ≥10 cm above the vegetation canopy and large enough to support a perching cowbird (≥15 mm; CAS, PA, KDO pers. obs.). We measured the distance from the nest to the nearest tree or shrub perch to the nearest 10 cm and measured the height of the nearest shrub perch to the nearest 1 cm. All measurements were made ≥10 days following fledging or nest failure, but before the vegetation had changed markedly with respect to the measurements above. Parasitized nests were those known to have received one or more cowbird eggs.

Statistical analyses.—We pooled data for all islands where cowbirds occurred. We excluded Mandarte Island from analyses presented here because intensive censuses and the absence of parasitized nests during the study period suggested that cowbirds did not visit the island. Results of analyses with and without nests from Mandarte Island included were similar. We also excluded nests initiated before cowbirds began laying in the study area because these nests were not susceptible to parasitism.

We used SYSTAT 9.0 for all statistical analyses (Wilkinson 1989). We used two sample *t*-tests to compare heights and distances because these variables were normally distributed. We used Mann-Whitney *U*-tests to compare percentages and counts because they were better suited to these kinds of data (Sokal and Rohlf 2000).

RESULTS

We collected data for 64 nests initiated after the arrival of cowbirds in the study area; 29 (45.3%) of these were parasitized. The probability of parasitism was positively related to nest exposure and the proximity of trees (Table 1). Unparasitized nests were less exposed than parasitized nests from both side and overhead views; however, the difference was significant only for side exposure. Distance to the nearest shrub perch was similar for parasitized and unparasitized nests, but parasitized nests were significantly closer to trees than unparasitized nests. The number of shrub perches within 10 m of nests was unrelated to parasitism, but there were nearly twice as many trees within 10 m of parasitized than unparasitized nests (Table 1). Only one parasitized nest had no trees within 10 m. Vegetation and

TABLE 1. Vegetation characteristics for 64 parasitized (n = 29) and unparasitized (n = 35) Song Sparrow nests on 10 islands (Mandarte Island excluded; see Methods) near Victoria, British Columbia. Parasitized nests were more exposed from the side and closer to trees than unparasitized nests. Values are means (SDs) and are compared by two-sample Mann-Whitney U-tests (exposure, number) or t-tests (distance, height). P-values are two-tailed and adjusted (×8) for the number of related tests.

Variable	Unparasitized	Parasitized	Test statistic (U or t)	P
Exposure (%)				
Overhead	23.4 (28.1)	42.1 (31.7)	2.50	0.120
Side	15.2 (13.6)	28.0 (19.5)	3.06	0.024
Distance (m)				
Shrub Perch	1.8 (1.8)	1.7 (1.8)	0.23	1.000
Tree	5.8 (2.5)	3.6 (2.4)	3.02	0.032
Number (within 10 m)				
Shrub Perches	8.2 (6.3)	11.5 (9.5)	1.63	0.872
Trees	2.5 (3.4)	4.7 (4.7)	2.21	0.248
Height (m)				
Nest	0.4 (0.4)	0.5 (0.4)	1.70	0.752
Vegetation	1.2 (0.5)	1.4 (0.8)	1.00	1.000

nest height were similar for parasitized and unparasitized nests (Table 1).

DISCUSSION

Our results support the Nest Exposure Hypothesis because well concealed Song Sparrow nests were parasitized less often, particularly those concealed from side views. Larison et al. (1998) also found that Song Sparrow nests within 1 m of the ground and with abundant lateral cover were parasitized less often than other nests, and suggested that the presence of dense lateral cover might conceal the movements of hosts near their nests and reduce the chance of detection by searching cowbirds. Our results are consistent with this suggestion. Strausberger (1998) suggested that cowbirds sometimes search for nests by hovering over the nest area, and many authors have suggested that cowbirds locate nests by observing hosts near their nest (see Hauber and Russo 2000). Our results strengthen the idea that the amount of cover near nests affects the ability of cowbirds to find them.

It is likely, however, that cowbirds use a variety of methods to find nests, and that the success of various methods or the frequency with which cowbirds employ them may differ with the type of habitat or host, or the density of hosts or cowbirds (Arcese et al. 1996, Brittingham and Temple 1996, Strausberger 1998, 2001). It is interesting that Hauber and Russo (2000) found no relationship between parasitism and the visibility of Song Sparrow nests in New York. In earlier work on Mandarte Island, Smith (1981), using a qualitative index of concealment (0–6 for completely exposed to concealed nests), suggested that parasitized nests were slightly, but not significantly, more exposed than unparasitized nests. Uyehara and Whitfield (2000) also found no relationship between nest concealment and parasitism in Southwestern Willow Flycatchers (*Empidomax traillii extimus*), where 57% of nests were parasitized. It is possible that high cowbird densities result in a higher percentage of host nests being parasitized and reduce the effect of vegetation cover (Robinson et al. 1995, Robinson and Smith 2000).

Our finding of a positive relationship between the proximity of trees and parasitism is consistent with earlier results of Clotfelter (1998) and Hauber and Russo (2000), and supports the Perch Proximity Hypothesis. However, Hahn and Hatfield (1995) found higher rates of parasitism in forest interior than in field or edge habitat and suggested that trees enhanced the ability of cowbirds to detect potential hosts without being detected themselves. Strausberger and Horning (1998), Strausberger (2001), and Strausberger and Burhans (2001) also have suggested that trees

provide vantage points from which cowbirds can observe nests undetected, and thereby avoid aggressive nest defense by hosts or lessen their rate of nest desertion. Song Sparrows often cease nest building when cowbirds are near (Arcese et al. 1996). Thus, the fact that we did not find a positive relationship between the presence or proximity of shrub perches and parasitism, but did find a positive relationship with the proximity to trees, suggests that trees are more important for the concealment that they provide than as vantage points. Clotfelter (1998) also noted that although proximity to trees was related to parasitism in Red-Winged Blackbirds (*Agelaius phoeniceus*), the number of perches near parasitized and unparasitized nests were similar.

Finally, we excluded from our analysis nests on Mandarte Island because the absence of cowbirds there during this study meant that nests were not at risk of parasitism. Since the colonization of the island by cowbirds between 1960 and 1975 (Smith and Arcese 1994), there has been a marked decline both in the number of trees on the island and the frequency of visits and rate of parasitism by cowbirds (CAS, PA, KDO unpubl. data). Given our current results, we suggest that Mandarte Island has become less attractive to cowbirds as the number of trees have declined and the vegetation structure has become less conducive to nest searching by cowbirds. This hypothesis predicts that tree encroachment into grasslands and old fields may increase the rate of parasitism in these habitats.

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VARIATION IN NEST SITES, NESTING SUCCESS, TERRITORY SIZE, AND FREQUENCY OF POLYGYNY IN WINTER WRENS IN NORTHERN TEMPERATE CONIFEROUS FORESTS

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ABSTRACT.—We studied the nesting ecology of Winter Wrens (*Troglodytes troglodytes*) from 1994–1996 in coastal, coniferous, temperate rain forest of southeastern Alaska. Overall nesting success (estimated by the Mayfield method) of 143 nests exceeded that reported for other published studies of temperate wrens, including *T. troglodytes*. Wrens used understory nest sites (logs, stumps, root disks of uprooted trees, understory moss, stream banks) in two forest sites where predation of nests was low (2% of 65 nests). Males at these two sites commonly had small territories (1.8 ha ± 0.3 SE and 1.2 ha ± 0.1 SE) and often mated polygynously (22% and 78% of males had at least two mates). In the third study area, where predation (probably by red squirrels, *Tamiasciurus hudsonicus*) on understory nests was relatively high (19% of 59 nests), nests most often were placed in moss clumps on tree branches, as high as 18 m above ground. Males in this study area had the largest territories (2.8 ha ± 0.4 SE) and most (90%) mated monogamously. Variation in nesting ecology among these three superficially similar (mature conifer forest) sites may be related to subtle differences in habitat features and predator abundance. *Received 12 September 2001, accepted 3 June 2002.*

The Winter Wren (*Troglodytes troglodytes*), an insectivorous understory passerine, occurs over a large geographical range, including both Eurasia and North America (Hejl et al. 2002). The ecology of this bird has been well studied in Europe, but has received much less attention in North America (Armstrong 1992, Hejl et al. 2002). Even though the Winter Wren is one of the most common birds in northern temperate coniferous forests of southeastern Alaska and coastal British Columbia (Arnott et al. 1995, Willson and Comet 1996), descriptions of its habitat use have been few (Heath 1920, McLachlin 1983, Waterhouse 1998, Van Horne and Bader 1990), descriptions of its nesting ecology have been limited to nest site selection (Waterhouse 1998), and no studies have documented nesting success.

We describe and compare nest placement, nesting success, territory size, and frequency of polygyny of Winter Wrens in several coniferous forest sites in southeastern Alaska and relate differences among populations, *a posteriori*, to differences among habitat features at these sites.

METHODS

Study area.—We conducted our study of Winter Wren nesting ecology during May through July, 1994–1996, in coastal, coniferous, temperate rain forest of southeastern Alaska. Our three primary study sites (45–60 ha), Peterson Creek and Fish Creek on Douglas Island, and Herbert River on the mainland, were located near the city of Juneau (58° 22′ N, 134° 35′ W). During the course of other field studies, we also recorded some wren nests at ancillary sites on the mainland near Juneau (Montana Creek, one nest; Sheep Creek, 14 nests), on Catherine and Baranof islands near Hanus Bay (57° 24′ N, 135° 00′ W; three nests), and on Kupreanof Island near Portage Bay (57° 00′ N, 133° 12′ W; two nests). Data from ancillary sites were used in general descriptions of nest site placement and in overall assessment of nesting success, but no comparisons were made with the three primary sites. The overstory vegetation of all sites except Sheep Creek was dominated by coniferous tree species, primarily western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), with some mountain hemlock (*T. mertensiana*) and yellow-cedar

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(*Chamaecyparis nootkatensis*), the latter especially on Baranof, Catherine, and Kupreanof islands. Tree species composition and forest structure differed among sites because of anthropogenic (logging) and natural forces (postglacial sediment deposition on alluvial floodplain). The Fish Creek and Peterson Creek sites were mature, uneven-aged spruce-hemlock forests from which selective logging approximately 80–90 years ago removed many dominant spruce (T. Pence pers. comm.). The terrain at Fish Creek was more rugged, characterized by rocky cliffs along the stream, and the forest had a more open understory than Peterson Creek. The Herbert River site was an even-aged, mature spruce forest on flat terrain between two glacial rivers (Herbert and Eagle rivers). Some selective tree harvest for construction of a mining road occurred about 50 years ago (T. Pence pers. comm.). The forest at Herbert River was dominated by mature spruce, with scattered black cottonwood (*Populus trichocarpa*), and some suppressed western hemlock in the understory. Red alder (*Alnus rubra*) was present along the streams at all three sites. Ancillary sites included low elevation mature coniferous forest, some selectively logged 30–80 years ago (R. Deal pers. comm.), uncut mature coniferous forests on moderate to steep slopes with small streams, and a deciduous valley with small coniferous forest patches (see Willson and Comet 1996 for description). The understory vegetation used by wrens for nest cover or foraging in coniferous forest sites generally consisted of yellow skunk cabbage (*Lysichiton americanum*), blueberry (*Vaccinium* spp.), devil's club (*Oplopanax horridum*), salmonberry (*Rubus spectabilis*), currants (*Ribes* spp.), elderberry (*Sambucus racemosa*), rusty menziesia (*Menziesia ferruginea*), and a variety of mosses (see Alaback 1982).

We measured the relative abundance of potential nest sites within most nesting territories (see territory sizes, below) during 1996 by counting the number of potential nest sites (i.e., understory wood: logs, stumps, and root disks of uprooted trees; understory moss: moss skirts at the bases of tree trunks and moss-covered mounds on the ground; and arboreal moss: clumps of moss hanging from tree branches) in 20 5-m radius plots selected arbitrarily throughout each territory. We also measured the length of stream bank suitable for nesting within each territory. We judged potential nest sites based on the kinds of sites used for nests during previous years. We also used these data to derive a general description of the habitat at each of the three main study sites. During 1998, we determined the species and dbh of all trees taller than 1.3 m along four 200-m transects (nine 5-m radius plots per transect; 2,826 m^2 sampled per site) positioned ≥200 m apart at the three main study sites.

Nest monitoring.—Our nest-searching effort varied among years. During 1994, while conducting another study we documented wren nests at two of the three main study sites (Peterson Creek and Herbert River). We focused on wren nesting ecology at Fish Creek and Herbert River during 1995 and at Herbert River, Peterson Creek, and Fish Creek during 1996. Nest searches began at first light (approximately 03:00 AST) and continued until approximately 12:00. During each year, 6–10 observers searched for nests on 40–60 days.

Most nests (85% of 143 with known outcome) were accessible and we checked their contents every 1–3 days; we determined the status of inaccessible nests (n = 21) by observing nesting behaviors of adults. We considered a nest to be (1) active if adults were observed tending eggs or young, (2) depredated if the nest showed obvious signs of depredation (eggshell fragments or torn nesting material), (3) failed due to weather if the nest showed obvious signs of disturbance from rain or flooding, (4) abandoned if the nest was not tended and cause of failure was unknown, or (5) successful if adults were observed feeding at least one young of known (for nests with known hatch dates) or estimated (based on appearance of young) fledging age (in this study: 16.0 days ± 0.6 SE, n = 12). We located fledglings within territories within 2 days after fledging to verify that fledging had occurred. We excluded from analyses nests abandoned during nest building and those not used for reproduction.

We used the Mayfield method (Mayfield 1975) with modifications of Hensler and Nichols (1981) to calculate nesting success, excluding seven nests with unknown outcomes. We used mean values for clutch sizes (5.6 eggs ± 0.2 SE, n = 11), incubation pe-

riods for complete clutches (16.0 days ± 0.9 SE, $n = 4$), and nestling periods (16.0 days ± 0.6 SE, $n = 12$) to determine observation days during each period of the nesting cycle. For calculations of percent nesting success, we included a 21-day period for egg laying and incubation (assuming incubation begins on the day of clutch completion), and a 16-day nestling period. Unless otherwise stated, all values of nesting success are estimates using the modified Mayfield calculation.

After a nest failed or the young fledged, we measured nest height above ground and (during 1995 and 1996 only) the percentage of vegetative cover around the nest. We determined lateral vegetative cover by using a clear plastic board divided into 25 1-cm squares. The nest was placed centrally within the grid held 1 m from the nest and 1 m in front of the observer's face. From each of the four cardinal directions, we determined the amount of vegetation obscuring the nest by counting the number of squares that were >50% filled by vegetation in front of the nest. We used the mean percent cover at the four cardinal directions to represent overall nest cover. We also measured nests with unknown outcomes and included the data in general descriptions of nest site use. Some nest measurements could not be obtained because nests were inaccessible to us or were still active during the last nest visit.

Territory sizes and pairing status.—During 1996, using mist nets and a tape recording of another male's territorial song, we captured and banded adult wrens (16 males and four females) to allow for identification of nest and territory ownership and pairing status (i.e., monogamous or polygynous). Individuals were banded with a USFWS aluminum band and a unique combination of plastic colored leg bands (Avinet, Dryden, New York). Once a nest was located, we began to delineate that male's territory by spot mapping singing males, territorial disputes, foraging activity, and interactions with females. We next located the nest(s) and determined the territory boundaries of the neighboring male wren. Multiple observers then simultaneously followed neighboring males for at least a 2-h period on each of five days to clarify boundaries. We also documented territory boundaries and pairing status for 11 unbanded males. Most male wrens (24 of 27) had neighbors, and territories of unbanded males always were adjacent to banded males; using adjoining territories of males with active nests allowed us to better define territory boundaries (see Bibby et al. 1992).

The size of one territory was not estimated because the boundaries of his neighbors' territories were unknown. Males with multiple, concurrently active nests and males that tended fledglings and nestlings simultaneously were considered polygynous. Because few females were banded, we were unable to document sequential polygyny. Thus, for the purposes of this study, polygyny refers only to simultaneous polygyny.

To determine nest site selection, we tested for differences between distributions of nest site use and potential nest site availability within sites with log likelihood G-tests (Sokal and Rohlf 1995) for each of the primary study sites. If a significant difference was obtained, we constructed a 95% confidence interval for proportions of used sites and compared it to proportions of available sites to determine if nest sites were favored, avoided, or used in proportion to availability (Byers et al. 1984). We used the computer program CONTRAST, which uses a chi-square analysis with multiple comparisons (Hines and Sauer 1989) to analyze Mayfield daily survival rates. We used stepwise regression analysis with an entry criterion of 0.15 (SAS Institute, Inc. 2000) to examine relationships between territory sizes and availability of potential nest sites. We angular transformed all percentage data prior to analysis with parametric statistics and used a square root transformation on the potential nest site availability data because group variances were proportional to means (Zar 1999). For multiple comparisons, we used an adjusted alpha value to control for experimentwise error (Zar 1999).

RESULTS

Habitat features of main study sites.—Density of all tree species combined did not differ significantly among study sites, but the forest at Herbert River was characterized by more spruce and less hemlock of all size classes than the forests at Peterson Creek or Fish Creek (Table 1). Overall, Peterson Creek had the most downed wood in the understory (Ta-

TABLE 1. The density of trees did not differ significantly among the three main study sites in southeastern Alaska, 1998, but the Herbert River site was characterized by more spruce and less hemlock of all size classes than the other two sites. Values are mean ± SE number of trees per ha.

	Fish Creek	Herbert River	Peterson Creek	*F*	*P*
Sitka spruce	136 ± 66[a]	611 ± 79[b]	321 ± 73[a]	10.98	0.004
Western hemlock	650 ± 123[b]	107 ± 60[a]	611 ± 147[b]	6.82	0.016
Black cottonwood and red alder	0 ± 0	19 ± 7	7 ± 4	3.80	0.064
All tree species	926 ± 74	850 ± 96	1093 ± 17	1.10	0.375

[a,b] Means within a row with different superscripts are significantly different (ANOVA with Tukey's pairwise test; SAS Institute, Inc. 2000).

ble 2), where large decaying stumps and logs were common. There were fewer uprooted trees in the understory at Herbert River than at Fish Creek or Peterson Creek. The Herbert River site had the greatest abundance of thick mats of moss hanging from tree branches but the least amount of moss on the ground or on the bases of tree trunks. The Peterson Creek site provided much suitable stream bank whereas Herbert River provided very little.

Nest site selection and nesting success.— Most wren nests (143 of 150) were placed within cavities. Cavities most often were formed in moss growing on tree branches (54 nests), tree trunks (10 nests), decaying wood (7 nests), or on banks, cliffs, or the ground (12 nests). Wrens also used cavities in decaying logs, snags, and stumps (30 nests), live trees (five nests), and earthen banks (25 nests). Seven nests were built outside of a cavity, placed on tree branches or directly on the ground beneath logs or shrubs.

The distribution of nest site placement differed significantly (all $P < 0.005$) from potential nest site availability at all study sites (all df = 3; Herbert River: $G = 27.7$; Fish Creek: $G = 55.1$; Peterson Creek: $G = 48.2$; Fig. 1). Most nests at Herbert River were in moss clumps on tree branches, proportional to availability, and bank nest sites, although rare, were favored. Most nests at Fish Creek were in understory wood and understory moss, in proportion to availability; moss clumps on branches, although fairly abundant, rarely were used. Most nests at Peterson Creek were in stream banks, although this type of site was relatively less abundant than moss clumps on tree branches.

Only at Herbert River did wrens consistently place nests ≥2 m above ground (mean nest heights: 6.9 m ± 0.8 SE, $n = 59$ at Herbert River; 1.1 m ± 0.1 SE, $n = 24$ at Fish Creek; 2.2 m ± 0.7 SE, $n = 43$ at Peterson Creek), despite availability of alternative nest sites in the understory (Table 2). The difference in nest height among sites was significant (ANOVA: $F_{2,124} = 18.48$, $P = 0.0001$; and Tukey's pairwise test, $P < 0.05$).

TABLE 2. Availability of potential nest sites for Winter Wrens differed among the three main study sites, southeastern Alaska, 1996. Values (except bank) are mean (± SE) relative abundances of all plots sampled within a site and are represented as mean number per m^2 of habitat. Values for bank are means of territories within sites and are expressed as m of bank per ha of territory.

Potential nest site	Herbert River	Fish Creek	Peterson Creek
Understory wood	2.3 ± 0.2[a]	2.1 ± 0.2[a]	4.4 ± 0.2[b]
Log	1.1 ± 0.1[a]	1.2 ± 1.1[a]	1.9 ± 0.2[b]
Stump	1.0 ± 0.1[b]	0.6 ± 0.1[a]	2.0 ± 0.1[c]
Root disk of uprooted tree	0.2 ± 0.04[a]	0.4 ± 0.1[b]	0.5 ± 0.1[b]
Arboreal moss (no. mossy branches)	15.4 ± 1.3[c]	3.9 ± 0.6[a]	8.2 ± 1.0[b]
Understory moss (mossy trunk bases, mossy ground mounds)	2.1 ± 0.1[a]	3.3 ± 0.2[b]	5.5 ± 0.3[c]
Earthen bank	7.2 ± 3.6[a]	47.8 ± 10.9[a]	398.0 ± 44.4[b]
No. plots (territories) sampled	160 (8)	200 (10)	160 (8)

[a,b,c] Means within a row with different superscripts are significantly different (ANOVA and Tukey's pairwise test; SAS Institute, Inc. 2000).

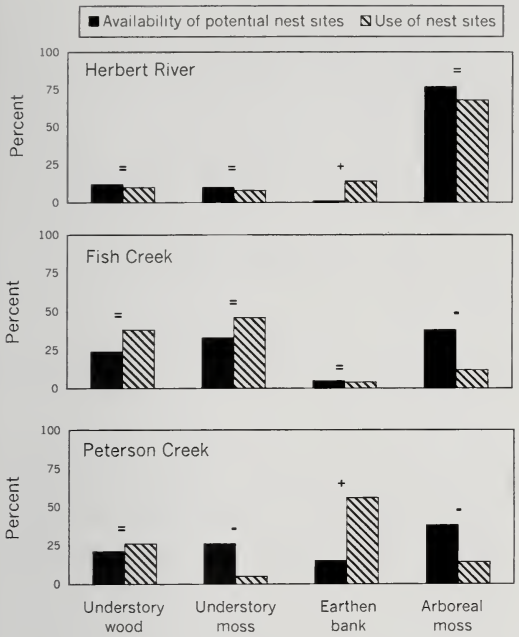

FIG. 1. Nest-site availability differed significantly from nest-site use (by G-test and simultaneous confidence intervals as described in Byers et al. 1984) by Winter Wrens at the three main study sites, southeastern Alaska, 1994–1996. Symbols indicate whether nest site type was selected (+), avoided (−), or used in proportion to availability (=). Sample sizes are 59 nests at Herbert River, 24 at Fish Creek, and 42 at Peterson Creek.

Only 19 (13%) nests with known outcome (n = 143) failed, and 12 of these failures were due to predation (Table 3). Daily mortality due to predation differed significantly among sites (χ^2 = 17.0, df = 2, P = 0.0002) with highest mortality at Herbert River, where 11 (92%) predation events occurred (Herbert River versus Fish Creek: χ^2 = 16.0, df = 1, P = 0.0004; Herbert River versus Peterson Creek: χ^2 = 9.80, df = 1, P = 0.0034; Fish Creek versus Peterson Creek: χ^2 = 1.0, df = 1, P = 0.62). Only three nests failed because of weather (i.e., flooding) and all were at Peterson Creek, where nests often were placed in the bank directly above the stream. The cause of the remaining five failures was unknown.

There was no significant difference in daily nest survival among years (χ^2 = 0.52, df = 2, P = 0.77). Therefore, subsequent analyses were pooled over years. Nest predation was similar during the incubation (daily mortality: 0.007% ± 0.003 SE) and nestling stages (0.003% ± 0.001 SE; χ^2 = 1.60, df = 1, P = 0.21; within-site tests were not conducted because all but two predation events occurred at Herbert River).

In general, successful nests were higher above ground (4.4 m ± 0.5 SE, n = 124) than depredated ones (2.2 m ± 0.8 SE, n = 13; t = 2.33, df = 135, P = 0.029), but there was no significant difference in density of foliage surrounding nests (percent vegetative cover

TABLE 3. Winter Wren nesting success (by modified Mayfield estimate) was high in general, but predation did account for some nest failure, particularly at one of the three main study sites, southeastern Alaska, 1994–1996.

	Herbert River	Fish Creek	Peterson Creek	Ancillary sites	All nests, all sites
Number of nests (n)					
with known outcome	59	24	41	19	143
successful	47	22	37	18	124
failed	1	2	3	1	7
depredated	11	0	1	0	12
Observation days (n)					
incubation period	564	131	275	78	1,048
nestling period	759	307	481	188	1,735
Daily nest survival (mean ± SE)					
From predators	0.992 ± 0.002	1 ± 0	0.999 ± 0.001	1 ± 0	0.995 ± 0.001
All causes of failure	0.991 ± 0.003	0.995 ± 0.003	0.995 ± 0.003	0.996 ± 0.004	0.993 ± 0.002
Overall percent nesting success	69.2	80.8	76.8	76.3	72.9

TABLE 4. Monogamous and polygynous Winter Wrens experienced similar nesting success at the three main study sites, southeastern Alaska, 1996. There were no significant differences between daily nest survival of monogamous and polygynous pairings of banded birds ($\chi^2 = 0.08$, df = 1, $P = 0.78$) or pooled data including both banded and unbanded males ($\chi^2 = 0.12$, df = 1, $P = 0.73$).

	Number of successful nests (total nests)	Mayfield daily nest survival (observation days)
Monogamous pairings		
All males	15 (18)	0.992 ± 0.005 (308)
Only banded males	9 (11)	0.992 ± 0.005 (260)
Polygynous pairings		
All males	28 (31)	0.994 ± 0.003 (522)
Only banded males	17 (19)	0.994 ± 0.005 (309)

index; successful: 47.1% ± 4.0 SE, $n = 89$; depredated: 53.9% ± 11.9 SE, $n = 8$; $t = 0.72$, df = 95, $P = 0.47$). At Herbert River, where most of the predation events occurred, successful nests were significantly higher above ground (8.3 m ± 0.9 SE, $n = 47$) than depredated ones (2.4 m ± 0.9 SE, $n = 11$; $t = 4.51$, df = 56, $P = 0.001$) but had lower percent cover (19.9% ± 6.4 SE, $n = 30$ versus 50.7% ± 34.6 SE, $n = 7$, respectively; $t = 2.22$, df = 35, $P = 0.031$). Of the 11 predation events at Herbert River, 67% occurred at nests positioned in the understory (≤2 m of the ground); most nests were located much higher than 2 m (56% of nests were above 5 m). Nests in understory wood, understory moss, and banks at Herbert River were relatively more vulnerable to predators; over 30% of these types of nests were lost to predators versus only 8% of arboreal moss nests. In contrast, at Peterson Creek and Fish Creek, understory nests were common (over 80% of 67 nests), yet few (3%) were depredated.

Pairing status, territory size, and nesting success.—Overall during 1996, 37% of 27 male wrens were polygynous. Pairing status differed significantly among sites ($G = 13.53$, df = 2, $P = 0.001$). Most wrens at Herbert River (9 of 10) and Fish Creek (7 of 9) were monogamous, and all but one male at Peterson Creek ($n = 8$) had at least two females nesting on their territories. We noted one instance of trigamy at Peterson Creek and found no bachelors holding territories.

Territory sizes of males ($n = 26$) ranged from 0.7–4.8 ha (mean = 2.0 ha ± 0.2 SE). Mean territory size differed significantly among sites (2.8 ha ± 0.4 SE at Herbert River, 1.8 ha ± 0.3 SE at Fish Creek, 1.2 ha ± 0.1 SE at Peterson Creek; $F_{2,23} = 7.3$, $P = 0.004$); mean territory size at Herbert River was significantly larger than that at Peterson Creek or Fish Creek (Tukey's pairwise test, $P < 0.05$).

Polygynous males had significantly smaller territories (1.5 ha ± 0.2 SE, $n = 10$) than monogamous males (2.3 ha ± 0.3 SE, $n = 16$; $t = 2.2$, df = 24, $P = 0.038$). This relationship was largely a site effect, because most of the monogamous males were at Herbert River and most of the polygynous males were at Peterson Creek. There were too few polygynous males at Fish Creek and Herbert River, and too few monogamous males at Peterson Creek, to make within-site comparisons of territory sizes and pairing status. Monogamous and polygynous males experienced similar levels of nesting success (Table 4).

The stepwise regression analysis with territory size as the dependent variable entered only one independent variable, stream bank, into the model (parameter estimate = 0.003, SE = 0.001, $\chi^2 = 6.40$, $P = 0.011$). Territory size was inversely associated with this habitat feature.

DISCUSSION

In our study, nesting success was high (Mayfield estimated success of 73%; by simple percent, 87% of 143 nests fledged young), and exceeded that of all published studies of other northern Temperate Zone wrens: Bewick's Wren (*Thryomanes bewickii*; Kennedy and White 1996), Cactus Wren (*Campylorhynchus brunneicapillus*; Austin 1974), Carolina Wren (*Thryothorus ludovicianus*; Haggerty and Morton 1995), House Wren (*Trog-*

lodytes aedon; Li and Martin 1991, Johnson et al. 1993, Johnson and Kermott 1994), and Marsh Wren (*Cistothorus palustris*; Verner 1965, Leonard and Picman 1987). Furthermore, the nesting success we observed in southeastern Alaska exceeded that of this species in Europe (Garson 1980, Wesołowski 1983) and Idaho (Hejl et al. 2002). Predation was the most often mentioned cause of nest failure in all of these studies. In our study, nests in the nestling stage were not more vulnerable to predation than those in the incubation stage. Thus, chick begging apparently did not increase the risk of nest detection by predators, a result reported for other passerines as well (Cresswell 1997).

Despite high rates of nesting success in our study, predation was still an important risk, but only at the Herbert River site. Nearly all nests we found were placed in the understory except for those at Herbert River, where predation was relatively high. Most wrens at Herbert River nested in moss hanging from tree branches, and did so successfully. At Herbert River, nests near the ground were much more vulnerable to nest predators. A positive relationship between nesting success and height above ground has been found for other passerines as well (e.g., Li and Martin 1991). We also found that successful nests at Herbert River had less cover than unsuccessful ones, a result previously reported for the House Wren (Belles-Isles and Picman 1986, Li and Martin 1991). At the Herbert River site, nest cover and nest height probably were inversely related because nests built in moss hanging from tree branches were above the understory vegetation and, consequently, had little foliage cover. For wrens in our study, nest placement low to the ground was probably more influential than foliage cover in determining nest vulnerability.

The most probable nest predator at the Herbert River site was the red squirrel (*Tamiasciurus hudsonicus*; Sieving and Willson 1998). Squirrels harvest both hemlock and spruce cones but prefer the latter (O'Clair et al. 1997), which provide larger and more seeds (Pojar and Mackinnon 1994). Squirrels are far more abundant in spruce-dominated forests such as Herbert River than hemlock-dominated forests such as Fish Creek (TLD and MFW unpubl. data). Arboreal moss nests at Herbert River probably afforded more protection from squirrels than nest sites nearer the ground. Squirrels spend much time on the ground collecting, eating, and caching cones and are likely to encounter a nest placed in the understory. Squirrels also forage for cones in trees, but cones are produced primarily on upper branches (Burns and Honkala 1990), and wren nests are located on lower branches. A squirrel actively searching for nests probably would be less likely to discover an arboreal moss nest because of the overwhelming abundance of such nest sites at Herbert River scattered throughout a strongly three-dimensional environment. We postulate that by nesting in a type of site that was overwhelmingly abundant, diffusely distributed, and positioned out of the regular path of squirrels, arboreally nesting wrens decrease the likelihood of being discovered by this predator.

Territory sizes differed among the three main study sites. Other studies have reported territory sizes for *T. troglodytes* ranging up to 42 ha (Zimin 1972, Glue 1973, Lea and Bourne 1975, Hejl et al. 2002), with the smallest territories (<2.5 ha) associated with wet, wooded habitats (Armstrong and Whitehouse 1977, Steiof 1991), forests with an abundance of dead wood in the understory (Batten 1976; Wesołowski 1981, 1983; McLachlin 1983), and areas of high insect abundance (Cody and Cody 1972). We found territory size to be related to only one measured feature, stream bank, which was identified as an important element of nesting habitat.

The level of polygyny differed among study sites, with the level at one site, Peterson Creek, being much higher than other published reports (Armstrong and Whitehouse 1977, McLachlin 1983, Wesołowski 1987, Hejl et al. 2002). Polygyny is predicted to be more prevalent in areas where resources, such as food or nest sites, are abundant and unevenly distributed (Emlen and Oring 1977). The clumped distribution of stream bank nest sites at our study site with the highest polygyny may have facilitated resource monopolization and a high frequency of polygyny by male wrens at that site. Nest sites on moss-covered tree branches were abundant at Herbert River, but these sites, due to their uniform distribution across the habitat, probably were difficult to monopolize.

In some instances, females may select already mated males at least in part because they gain access to higher quality nest sites, as reported for House Wrens (Johnson and Searcy 1993). In our study, since some concurrently active nests within the same territory were as close as 30 m, it is unlikely that secondary females settled with already mated males because they were unable to discern the mating status of males prior to nesting.

The nesting ecology of Winter Wrens in southeastern Alaska appears to differ from that elsewhere, at least in terms of nesting success, nest site use, and level of polygyny. Furthermore, within southeastern Alaska, several aspects of nesting biology and measures of reproductive fitness differed in habitats that were superficially similar (mature coniferous forest). Wrens also nest in habitats in southeastern Alaska that are structurally very different from mature coniferous forest, such as clearcuts, regenerating second growth, and deciduous forest patches (Van Horne 1984, Kessler and Kogut 1985), where nesting ecology may differ from that in mature conifer forests. Studies of *T. troglodytes* in Europe also suggest that the reproductive ecology of this bird varies among populations in various habitats in a number of measurable ways (nesting success, territory size, pairing status; Wesołowski 1981, 1983, 1987; Armstrong 1992). Wrens nesting in deciduous forests in Poland had greater pairing success and smaller territory sizes than those nesting in coniferous forests (Wesołowski 1983), and territory size was inversely related to invertebrate prey abundance in Britain (Cody and Cody 1972). Clearly, it is necessary to examine a wide range of habitats to understand habitat relationships of Winter Wrens and it is not possible to extrapolate accurately from one or a few studies. The information presented here also suggests that altering the understory and forest structure may affect not only the density but also the reproductive ecology of this understory bird.

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DISTRIBUTION, ABUNDANCE, AND HABITAT AFFINITIES OF THE COASTAL PLAIN SWAMP SPARROW

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ABSTRACT.—We examined the distribution and abundance of the Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) at previously occupied sites and points within potential habitat. We found Swamp Sparrows throughout their formerly documented range except in southern Chesapeake Bay. Swamp Sparrows were most common in the Mullica River region of New Jersey where we detected individuals at 78% of systematically chosen points with a mean count of 4.1 birds/point. The percentages of points with positive detections in the regions of Delaware River (39%), eastern Delaware Bay (23%), western Delaware Bay (34%), and Tuckahoe River (31%) were lower. The mean count of birds/point was between 0.4 and 0.6 in these regions. A higher resolution Poisson model of relative abundance suggested that the greatest concentrations of Swamp Sparrows occurred not only in the Mullica River area but also along northwestern Delaware Bay. Regression analysis of Swamp Sparrow counts and habitat features identified shrubs (*Iva frutescens* and *Baccharis halimifolia*) as a key habitat component. By applying density estimates generated by DISTANCE (Thomas et al. 1998) to the approximate area of potential shrub habitat along Delaware Bay, we estimated that the core population of Coastal Plain Swamp Sparrows was less than 28,000 pairs. We recommend that the Coastal Plain Swamp Sparrow be listed as a subspecies of concern by state and local governments because of its relatively small population size, restricted distribution in the mid-Atlantic region, and narrow habitat requirements. *Received 23 April 2002, accepted 13 November 2002.*

The Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) is one of three subspecies of Swamp Sparrow, but unlike the more common races, *M. g. nigrescens* is restricted to a small region of the Mid-Atlantic coastal bay ecosystem. Originally described from specimens collected in the Nanticoke River marshes during 1947 (Bond and Stewart 1951), *M. g. nigrescens* occurs only in estuarine marshes of the upper Chesapeake and Delaware bays and in large river drainages along the Atlantic coast of New Jersey north to the tidal portions of the Hudson River (Greenberg and Droege 1990). Subsequent analysis has shown that *M. g. nigrescens* is morphologically distinct from all other Swamp Sparrows (Greenberg and Droege 1990). The *nigrescens* race is one of the few vertebrate subspecies endemic to the mid-Atlantic region, but investigations into its biology and status are lacking.

Within mid-Atlantic estuaries, Swamp Sparrows (*M. g. nigrescens* unless otherwise noted) are restricted to an often narrow band of shrubby habitat at the interface of upland and high marsh. This habitat is particularly susceptible to recent changes such as rising sea level, ditching, impoundment, the invasion of the reed *Phragmites australis*, and the development of roads, farm fields, and housing tracts. Studies conducted during the late 1980s identified breeding populations of up to 70 singing males at several sites in the upper Chesapeake Bay (RG unpubl. data). Subsequent visits to these and other sites with formerly documented breeding populations revealed marked reductions of Swamp Sparrow numbers in Maryland. Given significant declines of similar marsh-nesting subspecies, including the Cape Sable Seaside-Sparrow (*Ammodramus mirabilis*; Pimm et al. 1996), Dusky Seaside-Sparrow (*A. nigrescens*; Sykes 1980), and San Francisco Bay Song Sparrow (*Melospiza melodia* spp.; Marshall and Dedrick 1994), we undertook a standardized survey of the Chesapeake and Delaware bays to examine the current status of Coastal Plain Swamp Sparrows. We surveyed previously occupied sites and sites within potential

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breeding habitat to evaluate range changes, characterize habitat associations, identify regions of potential management importance, and generate baseline population estimates.

METHODS

Range prior to 2000.—We obtained records from the Breeding Bird Survey (1966–1999; Patuxent Wildlife Research Center, PWRC), state Breeding Bird Atlases (Delaware, 1983–1987; Maryland, 1983–1987; New Jersey, 1993–1997), published reports (Harlow 1907, Stone 1937, Stewart and Robbins 1958, Moore 1989, West 1993, Clapp 1997, McCann and Battin 1999, Hess et al. 2000), Maryland miniroute data, migration cards, nest records, stomach content cards (data at PWRC), specimen records (Univ. of California, Berkeley), and amateur birders throughout the study area (see acknowledgments). We considered only records from the coastal plain between 15 May and 31 August in order to avoid taxonomic confusion between *M. g. nigrescens* and migrants of other Swamp Sparrow races (Mowbray 1997). We surveyed sites previously occupied by Swamp Sparrows in order to characterize their current range more completely, but we did not include these data in regional comparisons.

Survey design.—We surveyed six distinct physiogeographic regions (Chesapeake Bay, Delaware River, western Delaware Bay, eastern Delaware Bay, Tuckahoe River, and Mullica River). We excluded regions in northern New Jersey and the Piedmont west of Chesapeake Bay because morphological characters of birds in these areas fall between those of *M. g. nigrescens* and *M. g. georgiana* (Greenberg and Droege 1990; RG unpubl. data). We also excluded marshes within Blackwater National Wildlife Refuge (NWR) and the remainder of southeastern Chesapeake Bay because at the time of this study few records existed for this region and the vast marshes would have been over represented in our sampling.

We identified potential marsh habitat along Chesapeake Bay and its major tributaries using USGS 1:24,000 topographical maps. We randomly allocated survey effort to these marsh sites proportionate to their area. To ensure adequate coverage of northern Chesapeake Bay, which has numerous and continuous records of Swamp Sparrows, we constrained our sampling by surveying 60 marsh sites north of Annapolis and 60 to the south. Of these, only 70 were accessible. We followed a similar method to identify 18 marsh sites along the Delaware River from Wilmington to Philadelphia.

Swamp Sparrow habitat use is poorly documented. When possible, surveyors located a point within shrubby brackish habitat (Greenberg and Droege 1990) at each marsh site in order to maximize the chance of detecting a Swamp Sparrow. In cases where sites were in close proximity, surveyors located points ≥400 m apart to prevent counting birds twice.

Along the shores of Delaware Bay, coastal marsh forms a continuous band of potential habitat. Therefore, in this area, we systematically assigned points at 400-m intervals along all roads traversing marsh habitat. Droege (1990) discussed the validity of extrapolating data from roadside surveys, but in our experience, roads in coastal marsh were similar to dikes or upland barriers, which were common in the managed wetlands surveyed. Along the western shore of Delaware Bay, we surveyed all accessible roadside points (n = 176) between Lewes and Delaware City. Along eastern Delaware Bay, we surveyed every other point from the Delaware Memorial Bridge east to the confluence of the Mullica and Wading rivers. Because of the geographical isolation of points in the Tuckahoe River (n = 16) and Mullica River (n = 9) areas, we considered these regions to be distinct from the eastern shore of Delaware Bay (n = 106 points). We did not survey the extensive marshes along the Atlantic Coast because prior records do not exist for this region and spot checking revealed no evidence of Swamp Sparrows.

Point counts.—We performed a single 10-min count at each point between 05:00 and 10:00 EST during periods of low wind (<29 kph) and no rain. We preferred wider sampling to replication since this is a more efficient means of reducing total variability in index surveys (Link et al. 1994). We conducted the survey between 25 May and 7 July 2000, the approximate period of peak singing (RG unpubl. data). Although singing decreased as pairs began nesting, behaviors associated with nesting (e.g., chipping and mobbing) helped maintain detectability. We mapped all Swamp

Sparrows detected within a 100-m radius, recorded substrate use when detected visually, and determined sex based on crown pattern and behavioral cues (Greenberg 1988). We used detections of Swamp Sparrows outside of the circle and outside of standard count periods in order to establish a more complete geographical range, but we excluded these observations from density estimates and comparisons of relative abundance. At each survey point, we estimated the percent area within a 100-m radius circle described by each of eight habitat categories: nonmarsh, open water, mudflat-beach, shrub, *Phragmites*, rush-reed-grass >0.5 m, rush-reed-grass <0.5 m, and other. Nonmarsh included forest, paved or gravel surfaces of roads, and farm fields. Other included broad-leaved emergent plants such as arrow arum (*Peltandra virginica*), pickerelweed (*Pontederia cordata*), and spatterdock (*Nuphar luteum*). We distinguished *Phragmites* from other reeds because it is structurally distinct (taller) and it is an invasive species whose presence has been implicated in the decline of other marsh species (Benoit and Askins 1999). Distinguishing between reeds and grasses of different heights served to grossly differentiate marshes dominated by short species such as salt-meadow grass (*Spartina patens*) and the short form of smooth cordgrass (*S. alterniflora*) from marshes dominated by taller species such as the tall form of smooth cordgrass.

Density.—We estimated density of Swamp Sparrows within the continuous band of habitat along Delaware Bay using DISTANCE (Thomas et al. 1998). Variance in counts between points in other regions was too high to make meaningful predictions. DISTANCE models detection probability as a function of distance between bird and observer, thereby accounting for potential decreases in detection efficiency with increasing distance from the observer. This approach assumes that detection is perfect within the smallest distance interval. We grouped observations into 20-m intervals to reduce the effects of error associated with observers' distance estimates. We used only detections of adult male birds within a 100-m circular plot to generate models for the eastern and western shores of Delaware Bay. The best model, selected using Akaike's Information Criterion (Akaike 1973), incorporated a uniform key function plus a cosine series expansion (Buckland et al. 1993).

Statistical methods.—We used SYSTAT 7.0 (SPSS 1997) to perform tests on data from randomly and systematically chosen points. Because of the nonnormal distribution of the data, we used the nonparametric Kruskal-Wallis test to judge regional differences in mean counts of birds. Differences were deemed significant if $P < 0.05$. We modeled the relationship between Swamp Sparrow counts and habitat variables using Poisson regression (Vincent and Haworth 1983), which is a special case of the General Linearized Model (McCullagh and Nelder 1989). We removed the covariate "other" from the model because habitat variables are compositional (i.e., the sum of fractional areas devoted to each habitat character is equal to one).

We created a map of relative abundance using a Poisson model with a spatially correlated random effect as described by Royle et al. (2001). Under this model, the correlation between expected count at any two sites decreases as an exponential function of distance between those sites. Relative abundance on the map represents the expected mean count that one would observe at a given location if suitable habitat exists.

RESULTS

Distribution.—The current distribution of Swamp Sparrows matches the distribution of past breeding season records except for the absence of birds along southern Chesapeake Bay. Swamp Sparrows occurred along the shores of Delaware Bay where suitable habitat exists (Fig. 1). The population extended into marshes of the Delaware River and the large rivers along the southern Atlantic coast of New Jersey but not along the Atlantic coast of Delaware.

We detected Swamp Sparrows at 78% of points ($n = 9$) in the Mullica River drainage and this rate of detection was significantly higher than in any other region (Table 1; $H = 18.043$, $P = 0.001$). No significant differences existed among other regions (Table 1). We did not include the Chesapeake Bay region in this test because some randomly chosen marsh sites included little or no habitat even though USGS maps indicated otherwise. Detection of Swamp Sparrows in this region was low (7%,

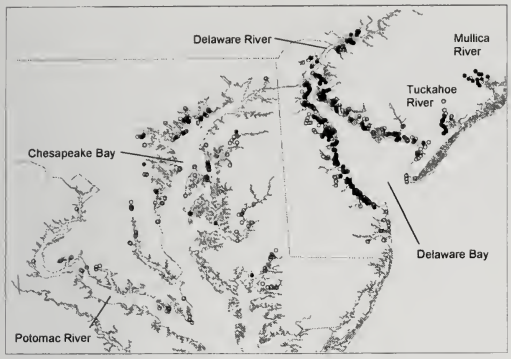

FIG. 1. Distribution of Coastal Plain Swamp Sparrows observed in 2000. Closed circles represent all records of Swamp Sparrows generated during point counts or otherwise. Open circles represent sites (randomly chosen or previously occupied) at which Swamp Sparrows were not detected during a 10-min point count.

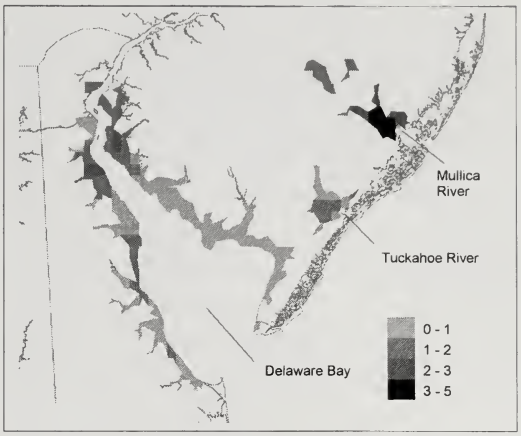

FIG. 2. Relative abundance of Coastal Plain Swamp Sparrows showing concentrated populations in the Mullica River region and northwest Delaware Bay. Shading corresponds to the number of males predicted to be detected during a 10-min point count in the major regions of estuarine emergent and shrub-scrub wetlands and palustrine emergent and shrub-scrub wetlands (National Wetlands Inventory; www.nwi.fws.gov).

0.1 birds/point, $n = 70$; Table 1). We located only 8 Swamp Sparrows in Chesapeake Bay during random surveys and we found only 4 by any means south of Annapolis.

Given the lack of specific habitat preference information for Swamp Sparrows, surveyors may not have conducted point counts in appropriate locations. Therefore, a regional comparison of Swamp Sparrow counts at points where at least one Swamp Sparrow was detected (i.e., occupied points) may be a better indicator of regional differences in distribution. Mean counts of birds at occupied points along the Mullica River (5.3 ± 1.6 SE) were significantly higher than in all other regions ($H = 15.214$, $P = 0.004$; Table 1). No significant differences existed among other regions.

A higher resolution map of relative abundance generated by a Poisson model of predicted counts revealed that areas of greater abundance extended farther to the mouth of Delaware Bay along the western shore compared to the eastern shore (Fig. 2). In addition, this model indicated that regions of high abundance occurred not only in the Mullica River area but also in the northwestern portion of Delaware Bay between Taylor's Bridge, Delaware, and Salem, New Jersey.

Habitat affinity.—Counts of Swamp Sparrows were significantly higher at plots with a greater proportion of shrub ($Z = 3.460$, $P < 0.001$; Table 2). The presence of open water

TABLE 1. Indices of abundance of Coastal Plain Swamp Sparrows based on 10-min, 100-m radius point counts performed in 2000. Counts and detection frequencies within the Mullica River region were significantly greater than in all other regions.

	All points				Points with at least one positive detection	
Region	*n*	% Points with positive detection	Maximum count	Mean count (± SE)	*n*	Mean count (± SE)
Chesapeake Bay	70	7	3	0.1 ± 0.1	5	1.6 ± 0.8
Delaware Bay (east)	106	23	5	0.5 ± 0.1	24	2.2 ± 0.5
Delaware Bay (west)	176	34	5	0.6 ± 0.1	60	1.7 ± 0.2
Delaware River	18	39	3	0.6 ± 0.2	7	1.6 ± 0.6
Mullica River	9	78	11	4.1 ± 1.3	7	5.3 ± 1.6
Tuckahoe River	16	31	2	0.4 ± 0.2	5	1.4 ± 0.6

TABLE 2. Relationship between counts of Coastal Plain Swamp Sparrows and habitat features as determined by a Poisson regression model. Swamp Sparrows were positively associated with shrubs, most commonly marsh-elder and saltbush.

Habitat feature	*Z*	*P*
Nonmarsh	−1.388	0.165
Water	−2.080	0.038
Beach-mudflats	0.244	0.807
Shrub	3.460	0.001
Phragmites	0.981	0.327
Reed-rush-grass < 0.5 m tall	−1.202	0.230
Reed-rush-grass > 0.5 m tall	0.220	0.826

correlated negatively ($Z = -2.080$, $P = 0.038$). The percentage of *Phragmites* in count circles correlated positively with Swamp Sparrow abundance, but not significantly (Table 2). Visual detections of Swamp Sparrows confirmed these habitat associations. Of 42 Swamp Sparrows observed directly, 33 were found in shrubs and eight in dead or living *Phragmites*.

Regional density and population estimate.—We estimated the density of male Swamp Sparrows along the eastern and western shores of Delaware Bay to be about 16/km^2 (95% CI = 10–23/km^2) and 37/km^2 (95% CI = 27–53/km^2), respectively. We generated these density estimates from plots where the mean percentage of unavailable habitat (roads, agricultural fields, forest) was about 20%. According to National Wetlands Inventory definitions (NWI; www.nwi.fws.gov), Swamp Sparrow habitat falls within four subclasses: estuarine persistent emergent, estuarine broad-leafed deciduous shrub-scrub, palustrine persistent emergent, and palustrine broad-leafed deciduous shrub-scrub. To generate a gross estimate of the core Swamp Sparrow population, we summed the area of wetlands of these four categories along the eastern and western shores of Delaware Bay (approximately 342 km^2 and 375 km^2 respectively; NWI) and multiplied by the density estimates above. This yielded a population estimate of 28,000 pairs, assuming a strong correlation between singing males and nesting females (Greenberg 2003).

DISCUSSION

We found the Coastal Plain Swamp Sparrow throughout its documented range, except along the southern Chesapeake Bay. We did not detect Swamp Sparrows along the Potomac River or the Patuxent River where birds had been observed only sporadically throughout the 1980s and 1990s. Similarly, we found little evidence of Swamp Sparrows at former breeding sites along the eastern shore of Chesapeake Bay, including the extensive Nanticoke marshes from which the type specimen originally was described. In contrast, breeding season records indicated continual occupancy along northwestern Chesapeake Bay since at least 1978. Within this region, we found small populations of Swamp Sparrows within the Patapsco River marshes south of Baltimore, in the area of Black Marsh and Hart-Miller Island, and in two locations on the Aberdeen Proving Ground. We found no evidence of large populations such as that observed by RG (unpubl. data) at Black Marsh during the 1970s.

We found several populations of Swamp Sparrows along the Delaware River, and a census of the John Heinz NWR at Tinicum revealed 22 pairs. Harlow, observing Swamp Sparrows near Philadelphia in the early 1900s, stated that "this species is the most abundant bird and nests in incredible numbers" (1907: 122). It is unlikely that our numbers reflect those described in Harlow's accounts.

Swamp Sparrows appeared to be most concentrated along the shores of Delaware Bay. Along the western shore, they occurred almost continuously from Lewes to Delaware City. The estimated density of 37 males/km^2 in this region, however, was low compared to 37–100 pairs/km^2 found during 1986 at Ted Harvey WMA (Moore 1989) and 125 territories/km^2 found during 1975 at Prime Hook NWR (West 1993). A Delaware Natural Heritage study at Woodland Beach found 189 territories/km^2 during 2000 (C. Heckscher pers. comm.). This disparity in density estimates probably is attributable to patchily distributed habitat and not fluctuating population sizes. We found Swamp Sparrows less frequently on the eastern shore of Delaware Bay (15 males/km^2), especially near Port Norris where previous occupation was well documented. On the other hand, we found high concentrations of Swamp Sparrows in the Mullica River for which we had no prior records of occupancy.

We observed Swamp Sparrows most com-

monly at the upland edges of marsh using marsh-elder (*Iva frutescens*) and saltbush (*Baccharis halimifolia*). We also found Swamp Sparrows in buttonbush (*Cephalanthus occidentalis*), red maple (*Acer rubrum*), and mallow (*Hibiscus* sp.) Dikes and roads traversing low marsh sometimes provided shrub habitat that may not have existed otherwise. In a few cases, we found Swamp Sparrows using wet fields adjacent to fresh or brackish tidal marsh. Plant species from these fields included switch grass (*Panicum virgatum*), plumegrass (*Erianthus giganteus*), sedges (*Carex* spp.), and beakrush (*Rhynchospora* sp.). A positive, but insignificant, correlation existed between Swamp Sparrows and *Phragmites*, a reed which forms dense, monotypic stands throughout coastal plain marshes. Male birds often used stalks as song posts and individuals sometimes foraged at the base of dead stalks.

Extensive, large tracts of Delaware Bay marsh are dominated by the short form of smooth cordgrass and salt-meadow grass. Though not significant, Swamp Sparrow counts correlated negatively with these short reed-rush-grasses. Canoe surveys throughout the low interior of marshes at Bombay Hook NWR and Mad Horse Wildlife Management Area corroborated this negative correlation (SD unpubl. data). Observations in the field suggested that the actual zone of suitable shrub habitat available to Swamp Sparrows typically extended only 200–400 m from the edge of the marsh-upland transition. Thus, our population estimate, which is derived from habitat estimates that include low marsh, probably is biased high.

We found only 34 Swamp Sparrows within the Chesapeake Bay region; however, subsequent searching indicates that several small populations exist in the Blackwater NWR (P. Marra pers. comm.). The extent to which the population penetrates the Pine Barrens (New Jersey) or extends north toward the Hudson River is undocumented at this time, but RG (unpubl. data) observed very few in Hudson Estuary tidal marshes. It currently is impossible to produce a rigorous global estimate of the Swamp Sparrow population. However, if we double our estimate of 28,000 (for the core Delaware Bay population) to 56,000 pairs to account for peripheral populations in the Chesapeake and northern New Jersey, then the Coastal Plain Swamp Sparrow population is on the same order of magnitude as that of the San Francisco region Song Sparrows (Marshall and Dedrick 1994), which have been designated federal subspecies of special concern.

Swamp Sparrows occupy a narrow band of vulnerable habitat within a limited geographic area. Coastal wetlands in the states of Maryland, Delaware, and New Jersey have declined by approximately 50% since the late 1700s (Dahl 1990) and development pressures will result in future habitat loss. In addition, the Environmental Protection Agency predicts a 50% chance that sea level will rise 58 cm at Lewes, Delaware, by 2100 (Environmental Protection Agency 1997). Rising water levels will inundate coastal wetlands and may threaten currently preserved habitat. A listing of the Coastal Plain Swamp Sparrow with other species of concern would facilitate the development of research and management initiatives before the subspecies reaches threatened or endangered status.

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POPULATION MONITORING OF PLAIN PIGEONS IN PUERTO RICO

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ABSTRACT.—The Plain Pigeon (*Columba inornata*) was listed as endangered in Puerto Rico in 1970. During 1986–1992 and 1997–2001, we collected point transect survey data to estimate density, population size, and rate of change. Density and population size estimates increased between 1986–1992 and 1997–2001. With a mean density of 0.25 ± 0.06 SE individuals/ha and a mean population size in the area of the surveys of 3,746 ± 892 SE individuals during 1997–2001, we believe that the status of the Plain Pigeon is not as precarious as it was during 1986–1992, when mean density was 0.02 ± 0.003 SE individuals/ha and mean population size in the area of the surveys was 218 ± 42 SE individuals. However, Plain Pigeons are not widely distributed and the loss and fragmentation of second growth forests combined with the effects of hurricanes and other factors may cause their extinction. Because Plain Pigeons have a spatially clumped distribution, we recommend sampling at least 1,195 points during peak nesting activity (March through June) throughout the island, with at least 526 points covering areas of abundance in eastcentral Puerto Rico, to monitor population changes and evaluate the effectiveness of management actions. *Received 24 June 2002, accepted 11 December 2002.*

Plain Pigeons (*Columba inornata*) are endemic to the Greater Antilles, where they are threatened or endangered mainly by habitat loss and hunting (Wiley 1985, Pérez-Rivera 1990, Strong and Johnson 2001). Plain Pigeons were common and widespread in Puerto Rico during the 1800s (Gundlach 1878, Wetmore 1916) but became nearly extinct between the 1920s and 1930s (Danforth 1931). They reportedly were hunted between the 1940s and 1960s, and a small population was found at the municipality of Cidra in eastcentral Puerto Rico in 1963 (Leopold 1963). Plain Pigeons endured a population bottleneck between the 1920s and 1960s (Miyamoto et al. 1994) and were listed as endangered in 1970 (U.S. Fish and Wildlife Service 1982).

As with many species listed under the Endangered Species Act (Tear et al. 1995), guesses and best estimates were used for listing Plain Pigeons. Between 1973 and 1983, counts conducted at Cidra fluctuated from 52–116 individuals (Wiley 1985), and the population was thought to be <200 individuals mainly restricted to eastcentral Puerto Rico (Pérez-Rivera 1977, 1981). *Ad hoc* estimates suggested that a population increase occurred between the 1970s and 1990s. For example, Lowe et al. (1990) reported a population of about 250 individuals, del Hoyo et al. (1997) reported about 300 individuals, Birdlife International (2000) reported about 700 individuals, and Oberle (2000) reported about 2000 individuals.

Reliable population parameter estimates are needed to establish recovery goals (Tear et al. 1995) and to assess population viability under adverse deterministic and stochastic processes, such as habitat loss and catastrophic weather (Lande 1993, Sæther et al. 1998). Standard sample surveys were conducted in Puerto Rico during 1986–1992 and 1997–2001 to estimate density, population size, and rate of change over time (Rivera-Milán 1992, 1993, 1995a; Martínez et al. 2001). Based on these parameter estimates, we assessed the population status of Plain Pigeons and make recommendations to continue monitoring trends as part of recovery efforts (U.S. Fish and Wildlife Service 1982, Puerto Rico Dept. of Natural and Environmental Resources 2000).

METHODS

Study area.—Puerto Rico, the smallest (880,190 ha) and easternmost (18° 15′ N, 66° 30′ W) island of the Greater Antilles, lies within the subtropical region, and has six life

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zones (Ewel and Whitmore 1973). Its forest cover increased from about 6% during the 1940s (Koenig 1953, Birdsey and Weaver 1982) to about 42% during 1991–1992 (Helmer et al. 2002). About 5% of the island area is protected, but rapid and widespread development is causing the loss and fragmentation of second growth forests (Birdsey and Weaver 1982, 1987; Ramos-González 2001; Helmer et al. 2002).

To collect survey data, we stratified the island according to the area of its three major life zones (dry zone = 121,640 ha, moist zone = 532,610 ha, and wet zone = 212,480 ha; Ewel and Whitmore 1973). Most of the forests in these life zones are characterized by second growth vegetation at different stages of succession (Birdsey and Weaver 1982). For example, early succession second growth forests in the moist zone are characterized by species such as trumpet tree (*Cecropia schreberiana*), American muskwood (*Guarea guidonea*), African tuliptree (*Spathodea campanulata*), and guaba (*Inga vera*).

Point transect surveys.—During each year of the study we conducted point transect surveys during peak nesting activity (March through June) on 8-km routes along secondary (paved) and tertiary (unpaved) roads covering all habitats used by columbids in the life zones. Depending upon topographic features (e.g., winding versus straight roads), the routes had 6–11 points (stations), with the first point of each route placed randomly and the others systematically at 800-m or 1,600-m intervals to minimize the chances of counting the same individuals more than once. We marked point centers so they could be found easily at all times. We used range finders to measure distances from point centers to Plain Pigeons detected singly or in flocks (clusters ≥2 individuals). Because we recorded distances to all columbids detected from point centers, distances were grouped into categories (0–15, 15–30, 30–45, 45–60, 60–90, 90–120, 120–180, 180–240, 240–340, 340–440, and >440 m) to secure data quality (Buckland et al. 1993).

We estimated density using the formula:

$$\hat{D} = n\hat{h}(0)\bar{s}/2\pi k,$$

where $\hat{D}$ = the number of individuals/ha; n = the number of individuals counted singly or in clusters; $\hat{h}(0)$ = the slope of the probability density function of detection distances, estimated at zero distance; $\bar{s}$ = mean cluster size; and k = the number of points sampled. At each point, two observers counted for 6 min all the Plain Pigeons seen or heard. We recorded distances to individuals flying overhead only if they were seen landing and their locations could be fixed before they started moving again. We recorded the distance from the center of a point to the center of a cluster of individuals or single individual up to 440 m. Detections beyond 440 m were recorded but not used for density estimation. Because columbids nest year-round (Wiley 1991; Rivera-Milán 1996, 2001; Rivera-Milán et al. 2003) and share a typical pattern of nest attendance (with males on the nest from midmorning to midafternoon or early evening, and females on the nest from late afternoon until midmorning of the next day; Blockstein and Westmoreland 1993), we conducted the surveys from 06:00–10:30 AST to include breeding and nonbreeding individuals of both sexes.

We used program DISTANCE (Thomas et al. 2001) to analyze the point transect survey data. We evaluated the fit of detection models (uniform, half-normal, and hazard-rate key functions with cosine, simple polynomial, and Hermite polynomial parameter adjustments) to data with χ^2 goodness-of-fit tests. Model selection was based on Akaike's Information Criteria (AIC or AIC_c; Burnham and Anderson 1998). Generally, data beyond 180 m were truncated to remove outliers and improve model fitting. If the regression of natural logarithm of cluster size ($\ln[s]$) and detection distance (r) was significant at $\alpha = 0.15$, we used the size-bias regression method to estimate mean cluster size. Encounter rate variance was estimated empirically. Based on data collected in eastcentral Puerto Rico from 1997–2001 ($k = 250$) and throughout the island from 1998–2001 ($k = 765$–$1,065$), we calculated the number of points (μ) needed to obtain a coefficient of variation (CV) of 20% for estimated density (Buckland et al. 1993: 304–307).

We used a one-tailed z-test (Thompson et al. 1998) to test the hypothesis that log-transformed estimates of density and population size of Plain Pigeons in eastcentral Puerto

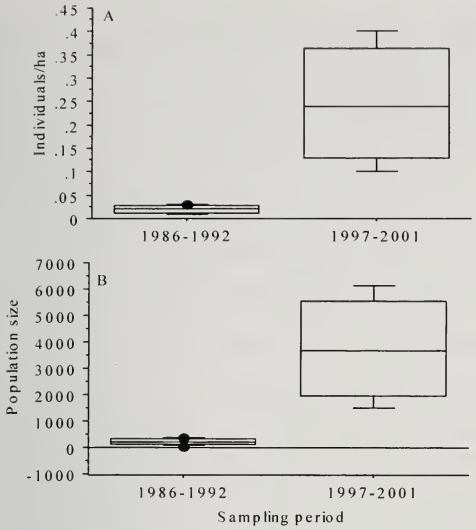

FIG. 1. Box plots of (A) density ($\hat{D}$ = the number of individuals/ha) and (B) population size ($\hat{N}$ = the number of individuals in the area of the surveys) estimates based on point transect survey data collected for Plain Pigeons in eastcentral Puerto Rico from March through June, 1986–1992 (k = 187) and 1997–2001 (k = 250). Percentile ranks (10th, 25th, 50th, 75th, and 90th) are shown, with the top and bottom of each box plot representing the 50th percentile, the line in the middle representing the median, the line extending above representing the 90th percentile and the line extending below representing the 10th percentile, and the circles extending from the lines representing values below the 10th percentile and above the 90th percentile.

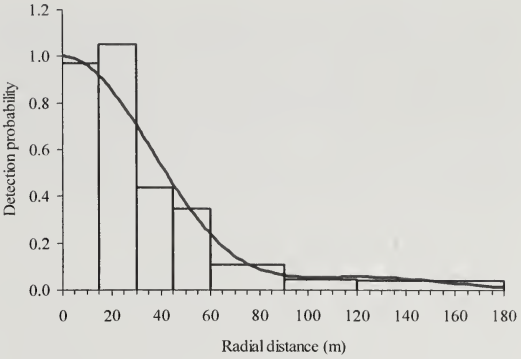

FIG. 2. Distance (r) and detection probability ($g[r]$) of Plain Pigeons based on point transect survey data collected on Puerto Rico during April through June, 2001 (n = 64 and k = 1,065). The half-normal key function + 2-term cosine parameter adjustments provided the most parsimonious fit to the data.

Rico were lower during 1986–1992 (k = 187) than during 1997–2001 (k = 250). To test for positive trends ($\hat{\beta}_1 > 1$) in log-transformed estimates, we used simple linear regression (Nur et al. 1999). Residual plots and residual statistics indicated that the assumptions of regression were met [e.g., ln(population size): Durbin-Watson d = 1.6, $P > 0.05$; serial autocorrelation = 0.2, Box Ljung Q = 0.7, P = 0.40].

RESULTS

Plain Pigeon density estimates ranged from 0.01–0.03 individuals/ha ($\bar{x}$ = 0.02 ± 0.003 SE) and population size estimates in the area of the surveys ($k\pi r^2$ = 11,374 ha) ranged from 60–377 individuals ($\bar{x}$ = 218 ± 42 SE) in eastcentral Puerto Rico during 1986–1992. Density estimates ranged from 0.10–0.40 individuals/ha ($\bar{x}$ = 0.25 ± 0.06 SE) and population size estimates in the area of the surveys ($k\pi r^2$ = 15,205 ha) ranged from 1,497–6,106 individuals ($\bar{x}$ = 3,746 ± 892 SE) during 1997–2001. Estimated density (z = −2.5, P = 0.007) and population size (z = −2.8, P = 0.002) were lower during 1986–1992 than during 1997–2001, respectively (Fig. 1). Rate of change was positive and significant (density: $\hat{\beta}_1$ = 0.29 ± 0.07 SE, t_{12} = 3.9, P = 0.001; population size: $\hat{\beta}_1$ = 0.33 ± 0.09 SE, t_{12} = 3.7, P = 0.002).

Plain Pigeons rarely were detected outside 24 routes (k = 187–250) in eastcentral Puerto Rico. In general, detection probability remained high in the first five distance categories (effective detection distance: $\bar{x}$ = 88 m ± 5 SE), cluster size ($\bar{x}$ = 1.8 ± 0.1 SE) was not related to detection distance, and the half-normal key function with cosine parameter adjustments fitted the data. For example, 64 detections were made in 1,065 points sampled from April through June, 2001, which resulted in a mean effective detection distance of 59 m ± 5 SE, a mean cluster size of 1.03 ± 0.02 SE (regression of ln[s] against r: B_1 = 0.0003 ± 0.0003 SE, t_{62} = 0.9, P = 0.83), and a half-normal key function with cosine parameter adjustments (m = 2) best fitting the data (AIC_c = 245.7; χ^2_4 = 2.3, P = 0.67; Fig. 2).

During 1998–2001 (k = 765–1,065), the coefficient of variation of density estimates ranged from 25–50% ($\bar{x}$ = 35% ± 0.5 SE) and the dispersion parameter estimate ($\hat{b}$) ranged

from 1.9–10.7 ($\bar{x}$ = 6.9 ± 1.8 SE). Because the spatial distribution of Plain Pigeons was clumped ($\hat{b} > 1$), we needed to sample at least 1,195 points throughout the island, with at least 526 points in eastcentral Puerto Rico, to obtain a desired coefficient of variation of 20% for estimated density.

DISCUSSION

In Puerto Rico, Plain Pigeons are multiple-brooded habitat generalists that feed on the fruits of a wide variety of plant species, mainly in mesic second growth forests (Pérez-Rivera 1978). Because density and food abundance are positively related (Rivera-Milán 1992, 1996, 2001; Bancroft et al. 2000; Rivera-Milán et al. 2003), we suggest that the recovery of second growth forests, particularly during the 1970s and 1990s, increased the quantity and quality of foraging and nesting habitats, which in turn elicited a positive population response in eastcentral Puerto Rico between 1986–1992 and 1997–2001. Forest area has increased since the 1940s because marginally productive pasture and cropland were abandoned as Puerto Rico gradually became industrialized (Koenig 1953, Birdsey and Weaver 1982, Helmer et al. 2002).

With a mean density of 0.25 individuals/ha and a mean population size in the area of the surveys of 3,746 individuals during 1997–2001, we believe that the status of the Plain Pigeon is not as precarious as it was during 1986–1992, when mean density was 0.02 individuals/ha and mean population size in the area of the surveys was only 218 individuals. Our optimism is tempered, however, because Plain Pigeons are not widely distributed and unmitigated development is causing major land cover changes (Ramos-González 2001, Helmer et al. 2002), which may be affecting the reproduction of Plain Pigeons through the loss and fragmentation of second growth forests in eastcentral Puerto Rico (Wiley 1985, Pérez-Rivera 1990, Rivera-Milán et al. 2003). Habitat changes may interact with catastrophic weather, food availability, nest predation, illegal hunting, and poaching of nestlings to reduce persistence, even when the population can be increasing exponentially (Mangel and Tier 1994). Illegal hunting, poaching of nestlings, and other forms of human-induced disturbance still occur (Ruiz-Lebrón et al. 1995) but not as frequently as during the 1970s (U.S. Fish and Wildlife Service 1982, Wiley 1985).

Hurricanes can affect plant and animal populations through multiple effects (Wiley and Wunderle 1994, Wunderle 1995, Lomascolo and Aide 2001). During 1986–2001, two hurricanes struck Puerto Rico: Hugo (a Category 5 hurricane based on the Saffir-Simpson scale) in September 1989 and Georges (Category 3) in September 1998. Hugo had stronger winds but Georges affected a larger portion of the island (for more information, see http://www.geocities.com/huracanado1/). Estimates of density and population size in November 1998 ($\hat{D}$ = 0.01 ± 0.01 SE and $\hat{N}$ = 310 ± 182 SE) were as low as during March through June, 1986–1992, remained depressed during February through October, 1999 ($\hat{D} \leq 0.10 \pm 0.03$ SE and $\hat{N} \leq 1{,}497 \pm 523$ SE), and rebounded to pre-hurricane levels during March through June, 2000–2001 ($\hat{D} \geq 0.12 \pm 0.04$ SE and $\hat{N} \geq 1{,}772 \pm 644$ SE).

As with other columbids (Rivera-Milán 1995b, Wunderle 1995), Plain Pigeons showed resiliency (Pimm 1991), and through successful reproduction responded rapidly to forest regeneration and increased food availability (Rivera-Milán 1996, 2001; Rivera-Milán et al. 2003). However, a hurricane with Hugo's wind force striking the island as did Georges can be devastating for Plain Pigeons. We hypothesize that extensive deforestation from agriculture (Koenig 1953, Birdsey and Weaver 1982), unregulated hunting pressure (Wiley 1985), and the passing through most of the island of hurricanes San Felipe (Category 5) in 1928 and San Ciprián (Category 3) in 1932, interacted to endanger an already reduced and patchily distributed population.

Reliable population monitoring data are needed to evaluate the effectiveness of management actions (Gibbs et al. 1999) and determine if recovery goals have been reached (Tear et al. 1995). Distance sampling theory provided an adequate framework to survey columbids using roads. In the case of the Plain Pigeon, this framework needs to reflect adjustments resulting from their spatially clumped distribution. This distribution may be the result of social behavior, reproductive adaptations, and habitat use with respect to the spatial and proportional distribution of foraging and nesting habitats. Plain Pigeons can

disperse long distances in search of food (Ruiz-Lebrón et al. 1995), but nesting has not been reported outside eastcentral Puerto Rico (Rivera-Milán 1996, 2001; Rivera-Milán et al. 2003). Because second growth forests have similar vegetation structure and composition in the moist zone, we do not know why they are not more widely distributed.

A spatially clumped distribution means that many points will have no detections whereas a few points will have detections of individuals or clusters of individuals. Depending upon the degree of clumping, sampling several hundred or thousand points may be required to obtain reasonably precise density estimates [$CV(\hat{D}) \leq 20\%$]. Currently, 1,065 points are sampled on Puerto Rico annually. This sampling effort is enough to obtain precise density estimates for abundant and widely distributed columbids, such as Scaly-naped Pigeons (*Columba squamosa*), Zenaida Doves (*Zenaida aurita*), and White-winged Doves (*Z. asiatica*). So, given the cost of conducting wide-ranging surveys, we suggest sampling at least 1,195 points throughout the island, with at least 526 points covering eastcentral Puerto Rico. Surveys should be conducted from March through June to cover the peak of nest density of Plain Pigeons and other columbids (Rivera-Milán 1996, 2001; Rivera-Milán et al. 2003). Surveys conducted from March through June (CV: $\bar{x} = 33\% \pm 2$ SE) were less variable than surveys conducted from July through February (CV: $\bar{x} = 47\% \pm 7$ SE) because of changes in flocking behavior (Rivera-Milán 1992, 1993, 1995a; FFR-M unpubl. data).

Plain Pigeons were detected easily and grouped into distance categories ranging from 0–15 m to 340–440 m. In general, detection probability remained high near point centers and decreased with distance, cluster size was not a function of detection distance, and detectability followed a half-normal process (Buckland et al. 1993). Plain Pigeons were detected near (0–30 m) and far (≥120 m) from roads because they frequently perched at canopy level and moved conspicuously within and between forest fragments. To be conservative, however, we did not estimate population size beyond the surveyed area ($k\pi r^2$) because placement of sampling units on or near roads may not be representative of their abundance in off-road habitats (Buckland et al. 1993, Thompson 2002). Further research is needed to validate sample inferences from on-road to off-road habitats (Keller and Scallan 1999).

Islandwide surveys would be impossible without the use of roads. Secondary and tertiary roads provide access to all habitat types used by columbids, ranging from upper montane wet forests to coastal dry forests. In Puerto Rico, Plain Pigeons behave as edge species (Yahner 1988), nesting, foraging, and roosting in trees at or near roads. Thus, we believe that point transect surveys along roads provided adequate coverage of their habitats and daily activities, and we recommend combining distance sampling with telemetry and geographic information systems to link demographic and spatial data. These data should be used to establish specific population and habitat recovery goals (Tear et al. 1995) for the downlisting and delisting of Plain Pigeons in Puerto Rico.

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SINGING BEHAVIOR OF MALE YELLOW-BREASTED CHATS: REPERTOIRES, RATES, REPRODUCTIVE SUCCESS, AND A COMPARISON WITH OTHER WOOD-WARBLERS

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ABSTRACT.—Previous authors have noted the unique singing behavior and apparently large song repertoires of male Yellow-breasted Chats (*Icteria virens*). We studied the singing behavior of 10 male chats in central Kentucky in an attempt to determine the size and functions of their song type repertoires and examine possible relationships among singing behavior, morphological characteristics, and reproductive success. During the 1995 breeding season, we recorded and analyzed chat songs and determined the morphological characteristics and reproductive success of focal males. Repertoire sizes varied among male chats, ranging from 46–81 song types. Larger males (as determined by tarsus length) had larger song type repertoires, and males with longer wing chords fledged more young. These relationships suggest a correlation between male quality (as determined by size and reproductive success) and repertoire size. Male chats spent less time singing after pairing, suggesting that singing plays a role in mate attraction. However, singing by male chats likely serves other functions, such as territorial defense and attracting additional mates, because males continued singing after pairing. In contrast to male wood-warblers (Parulidae), male chats have relatively large repertoires of song types and also vary the sequence of song types, the frequency of repetition of individual song types, and the length of time between consecutive song types. Such differences in singing behavior lend support to the hypothesis that chats are not parulids. *Received 4 January 2002, accepted 22 August 2002.*

The singing behavior of several species and genera of wood-warblers (Parulidae) have been examined, and these studies have revealed two different song systems (Spector 1992). In one system, shared by species in the genera *Protonotaria*, *Helmitheros*, *Limnothlypis*, *Seiurus*, *Oporornis*, and *Geothlypis*, males have a single primary song, plus a less commonly used extended song that includes portions of the primary song and some additional notes (Spector 1992). In the second system, shared by species in the genera *Vermivora*, *Parula*, *Dendroica*, *Mniotilta*, *Setophaga*, and *Wilsonia*, males have two distinct groups of songs; one group seemingly used primarily in intersexual contexts, and another used in intrasexual contexts (Spector 1992). While the singing behavior of most male parulids fits into one of these two song systems, the song systems of several species of parulids, including Yellow-breasted Chats (*Icteria virens*), have yet to be examined.

Based on anecdotal reports, some authors have suggested that the singing behavior of Yellow-breasted Chats may be unique among wood-warblers. For example, Morse (1989) noted that male chats may have repertoires of more than 100 songs. In describing the singing behavior of chats, Chapman (1917:267) reported that "the voice of this bird is flexible to an almost unlimited degree. It has no notes suggesting its place among the warblers." Bent (1953:593) stated that the chat's ". . . vocabulary is so extensive and varied that . . . it does not need to learn much from others."

The objective of our study was to examine the singing behavior of male Yellow-breasted Chats. Specifically, we wished to (1) determine the size of their song repertoires and how males used those repertoires, (2) determine possible functions of singing by examining singing rates throughout the breeding cycle and in different behavioral contexts, and (3) examine possible correlations among male singing behavior, morphological characteristics, and reproductive success.

METHODS

We studied Yellow-breasted Chats from 28 April through 19 August, 1995, at the Central Kentucky Wildlife Management Area located 17 km southeast of Richmond, Madison County, Kentucky (37° 37′ N, 84° 12′ W). This area consisted of fence rows, thickets,

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and small woodlots separated by cultivated and old fields. We captured chats in mist nets either by playing back chat songs or by placing nets in areas used by chats. We banded captured chats with a numbered aluminum band and a unique combination of colored plastic bands. We also measured wing chord and tarsus length.

We observed each focal male (n = 10) at least once every two weeks. Most observations were 1 h in duration and were conducted from sunrise to 11:00 EST. During focal male observations, we recorded all bouts of song using either a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone or a Marantz cassette recorder with a Mineroff directional shotgun microphone. We also spent several hours per week looking for nests. Once located, nests were checked at least twice weekly to determine stage and outcome. Because chats are multibrooded, we used the number of young fledged during the entire breeding season as a measure of reproductive success.

We analyzed recordings using a Kay Elemetric DSP SonaGraph (Model 5500). For each observation we determined the number of song types, new song types, singing rate (total number of song types given/duration of observation period), and the percentage of time spent singing (calculated by determining the total duration of all song bouts given during an observation period, dividing by the duration of the period, and multiplying by 100%). We also determined the extent to which song types were shared among seven male chats.

We defined a song type as either a single sound or a series of sounds where the interval between sounds was less than the time interval between successive song types. Song types were categorized based on differences in structure (appearance in a sonagram), duration, rate of delivery, and frequency at maximum amplitude. Chats consistently sang particular song types. For each male, all song types were identified and classified in a numeric directory (Derrickson 1987). Examples of four song types are provided in Fig. 1. When singing, male chats vary the sequence of four types and the length of time between consecutive song types. Thus, a song bout was defined as a series of song types in which the

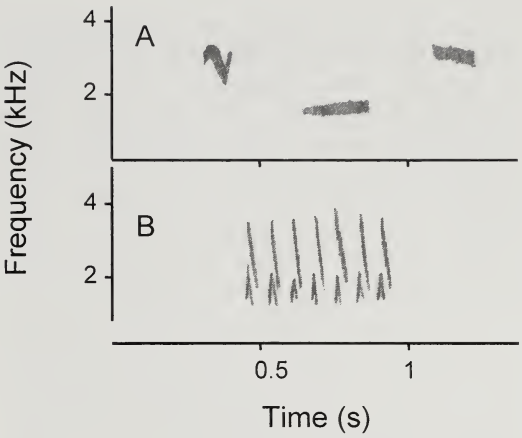

FIG. 1. Sonagrams of four song types given by male Yellow-breasted Chats (*Icteria virens*) in Madison County, Kentucky. (A) An example of three song types consisting of continuous sounds. (B) An example of a song type consisting of a series of sounds. Recorded by Natalie Dussourd, May 1995.

interval between song types was <15 s. Song types separated by >15 s were considered part of separate bouts.

To examine possible temporal variation in singing behavior, we divided the breeding season into six periods: pre-pairing, postpairing/prenesting, incubation, nestling, postfledging, and internesting (between nesting attempts). For pairs whose last nesting attempt of the season was unsuccessful, additional stages included either postnesting after losing a nest with eggs or postnesting after losing a nest with nestlings.

We determined song type repertoires for seven males, while 10 males were used for analyses of possible correlations between morphology and singing rates. We estimated the size of song type repertoires by plotting the cumulative number of new song types over the cumulative number of songs in a particular individual's repertoire and fitting a curve to the plot using the model $y = 1/x^2$. This model was used because it produced a higher r^2 value than several alternative models [$y = 1/x$, $y = e^{-x}$, and $y = \arctan(x)$]. The cumulative number of new song types at the asymptote of the curve was used as that individual's total song type repertoire. This model explained 92% of the total variance in the data, however, the residuals were not normally distributed (P = 0.0001). This was cor-

rected when the second and third observation periods of male LB1 were excluded from the analysis ($P = 0.106$). Male LB1 was the first bird on the study site and, because few other males had arrived on the study area, we observed him three times over a 2-day period. Because most other observation periods were separated by approximately two weeks, the inclusion of these observations apparently affected the normality of the residuals.

We calculated Pearson correlation coefficients for all predictor variables. To determine if there were differences among either breeding stages or males in singing rate and percentage of time spent singing, we used the general linear model repeated measures procedure. If significant differences were found, we used Tukey's studentized range test to determine which breeding stages or males differed. All statistical procedures were performed using the Statistical Analysis Systems (SAS) package (SAS Institute, Inc. 1989).

RESULTS

The estimated size of the song type repertoires of seven male chats ranged from 46–81 song types, with a mean of 62.2 ± 5.0 SE. Sharing of song types was common, with 50% of all song types shared by at least two males (41% among males in contiguous territories). Overall, male chats ($n = 10$) sang at a mean rate of 145.9 ± 20.4 SE song types/h and the mean time spent singing was 20.3% ± 3.1 SE ($n = 7$). Singing (song bout) rates did not vary significantly among breeding stages ($F_{6,19} = 1.54$, $P = 0.22$), however, time spent singing did vary among breeding stages ($F_{6,19} = 5.87$, $P = 0.001$; Fig. 2). Males sang more during the pre-pairing period than during the incubation, postfledging, internesting, and posteggs lost periods (Tukey's test; $P < 0.05$). Male chats also spent more time singing during the postpairing/prenesting period than during the postfledging period ($P < 0.05$).

The mean singing bout consisted of 4.2 ± 0.2 SE song types, with no significant difference in the number of song types per bout among breeding stages ($F_{5,9} = 2.96$, $P = 0.071$). Neither singing (song type) rates ($F_{6,19} = 0.29$, $P = 0.93$) nor time spent singing ($F_{6,19} = 0.28$, $P = 0.94$) varied significantly among the seven male chats. Similarly, we found no significant variation among males in mean bout length ($F_{6,9} = 2.49$, $P = 0.11$).

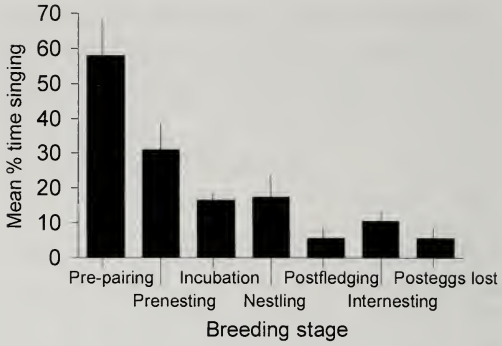

FIG. 2. Percentage of time spent singing by seven male Yellow-breasted Chats (*Icteria virens*) in Madison County, Kentucky, during different stages of the 1995 breeding season. Recorded by Natalie Dussourd.

We found few significant correlations between morphological characteristics and either singing behavior or reproductive success. However, male chats with longer wing chords fledged more young ($r^2 = 0.87$, $P = 0.010$). In addition, males with longer tarsi had larger song repertoires ($r^2 = 0.82$, $P = 0.023$).

DISCUSSION

The song type repertoires of seven male Yellow-breasted Chats in our study ranged from 46 to 81 types, and the positive correlation between tarsus length and song type repertoire size suggests that sexual selection may have played a role in the evolution of chat song repertoires. Females may be able to choose males that provide superior resources based on male repertoire sizes, which may reflect the age of males. In support of this hypothesis, we found that male chats with longer tarsi had larger song repertoires. Tarsus length may be a reliable indicator of male quality and size (older males are larger than younger ones; Lampe and Espmark 1994). The correlation between these two characteristics in chats may indicate that larger (and, thus, older and more experienced) males have larger repertoires and may be able to provide females and young with superior resources.

Sharing of song types.—Sharing of song types among male chats in our study was common. Such sharing may permit matched countersinging, with one male singing a particular song type and another male responding

with the same song type (Krebs et al. 1981). Matched countersinging may play a role in territorial interactions and in conveying dominance status (Krebs et al. 1981, Kroodsma 1979). A related suggestion is that matching is a "keep out" signal directed at a specific intruder (Armstrong 1973).

Singing rates.—In many passerines, male singing rates decline after pairing (Wasserman 1977, Gottlander 1987), suggesting that singing functions primarily to attract females. Although the singing rates of male chats in our study did not decline after pairing, the time spent singing did. This decline in time spent singing after pairing suggests that singing by male chats serves to attract mates. The continued singing by males after pairing, however, also suggests additional functions, including territorial defense. Male chats respond aggressively to playback of the songs of conspecific males (Ritchison 1988) and display flights accompanied by song occur during territorial disputes (Eckerle and Thompson 2001), suggesting that singing serves to maintain territory boundaries (Eckerle and Thompson 2001). Singing by male chats also may serve to attract additional mates. Although predominantly socially monogamous, the mating system of chats ranges from monogamy to successive monogamy to polygyny (Thompson and Nolan 1973). Males may, therefore, continue singing to attract a second female (McDonald 1989). One male chat in our study was polygynous (with two females), and this male also had the largest song repertoire of all focal males and was the first to arrive on our study site.

Chats in our study population did engage in extrapair copulations (Mays 2001). Thus, singing by male chats also might function to solicit extrapair copulations from neighboring females. Singing also may represent a form of mate guarding. For example, male Yellowhammers (*Emberiza citrinella*) announce the fertility status of their mate via song. Males that sang at higher rates experienced fewer territorial intrusions by neighboring males than those that sang at lower rates (Møller 1991). Because male and female chats do apparently solicit extrapair copulations, males may sing to prevent territorial intrusions by neighboring males attempting to copulate with their females.

Singing behavior, morphology, and reproductive success.—Male chats with longer wing chords fledged more young, and males with longer tarsi had larger song repertoires. Measures of body size, such as wing chord and tarsus length, may be good indicators of male quality (Lampe and Espmark 1994). Larger males would have smaller constraints placed on temperature and energy requirements (Morse 1989). A larger individual also may be more likely to win territorial disputes (McGregor et al. 1981, Searcy and Andersson 1986) and thus maintain a better territory. Female reproductive success is affected by territory quality in many passerines (Searcy 1982, Searcy et al. 1985). The significant correlations between tarsus length and repertoire size and between wing chord and number of fledglings suggests that male chats of higher quality may have larger repertoire sizes and fledge more young. Thus, females may use singing ability as an indicator of male quality. Similarly, blacker (and thus older and more experienced) male Pied Flycatchers (*Ficedula hypoleuca*) have longer wings (Slagsvold and Lifjeld 1988), more complex songs (Lampe and Espmark 1994), and survive better (Slagsvold and Lifjeld 1988). Several studies of other species, however, have revealed no such correlations between singing behavior and male quality (Lambrechts and Dhondt 1986, Bijnens 1988, McGregor 1988).

Comparison with other wood-warblers.—The singing behavior of male Yellow-breasted Chats in our study differed from that described previously for wood-warblers (Spector 1992). Male chats, in contrast to male wood-warblers, possess relatively large repertoires of highly variable song types (this study; Eckerle and Thompson 2001). Also, in contrast to male wood-warblers, male chats vary the sequence of song types, the frequency of repetition of individual song types, and the length of time between consecutive song types (Eckerle and Thompson 2001; ND and GR pers. obs.). Finally, male chats, in contrast to wood-warblers, may incorporate the songs and calls of other species into their repertoires (Kroodsma and Baylis 1982). Because singing behavior can suggest relationships among taxa (Spector 1992), such differences between Yellow-breasted Chats and other wood-warblers suggest possible phylogenetic differences. The

taxonomic placement of chats has generated considerable controversy (Eckerle and Thompson 2001). Recent work, however, suggests that several genera traditionally assigned to the Parulidae, including *Icteria,* probably are more closely allied to other nine-primaried oscine families (Lovette and Bermingham 2002). Specifically, mtDNA-based and *c-mos* reconstructions suggest that Yellow-breasted Chats may be allied to a group of icterids, particularly *Dolichonyx* (Lovette and Bermingham 2002). Similarly, Klicka et al. (2000), based on analysis of mitochondrial cytochrome-b and NADH dehydrogenase subunit 2 genes, reported that *Icteria* grouped with either *Dolichonyx* or *Sturnella*. Thus, our results support a growing body of evidence that Yellow-breasted Chats are not allied to the Parulidae.

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FIGHTING IN FEMALE MAGELLANIC PENGUINS: WHEN, WHY, AND WHO WINS?

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ABSTRACT.—Female Magellanic Penguins (*Spheniscus magellanicus*) fought for the best quality nests, mainly before egg laying. Female fights (n = 47) were longer than male fights (n = 138), but less frequent and less intense as indicated by the number of flipper hits and length of cuts. Female winners occupied the disputed nests, and losers usually moved to nests of lower quality. Losers subsequently fledged fewer chicks than winners. Female winners were in better body condition, were not significantly larger, and were the owners of the nest as indicated by previous season attendance at the nest. *Received 17 April 2002, accepted 22 September 2002.*

Aggression among female birds is less studied than among males; however, several studies suggest that female aggression could be widespread in birds (Yasukawa and Searcy 1982, Rätti et al. 1994, Liker and Székely 1997, Sandel and Smith 1997) and could affect mating systems and parental care (Liker and Székely 1997). Female birds fight for nests or territories (Chek and Robertson 1991), for mates (Stephens 1982, Freed 1986, Hotta 1994), to exclude other females from laying eggs in their nests (Møller 1987), or to avoid sharing their mate (Yasukawa and Searcy 1982, Liker and Székely 1997, Sandel and Smith 1997).

Game theory models predict that the willingness of individuals to fight should vary according to the value of winning a resource. Females therefore should be more aggressive when the potential benefits of winning are relatively high (Maynard Smith and Parker 1976, Hammerstein 1981, Parker and Rubenstein 1981, Hammerstein and Parker 1982). Furthermore, game theory models suggest arbitrary rules such as "owners win" could be an evolutionarily stable strategy (ESS) when the benefits of winning a fight are low relative to fighting costs (Maynard Smith and Parker 1976). When payoffs of winning are high for at least one of the contestants an ESS is unlikely, because individuals that break the rules benefit. Thus, when payoffs are high models predict disputes should be determined by asymmetries in fighting ability (also known as resource holding potential) or asymmetries between contestants in the value of the disputed resources (Parker 1974, Maynard Smith and Parker 1976, Enquist and Leimar 1983, Leimar and Enquist 1984). When asymmetries in fighting ability or resource value are used to settle contests, individuals should evaluate these asymmetries during the fight and use this information to determine whether to retreat and avoid further injury, or to continue fighting. As a consequence, when differences in fighting ability between contestants and differences in how the individuals value the disputed resources are small, fight duration should increase (Parker 1974, Enquist and Leimar 1983).

We describe fights between female Magellanic Penguins (*Spheniscus magellanicus*) and assess the predictions of game theory models that the benefits of winning determine the outcome and severity of fights. Magellanic Penguins are colonial monogamous seabirds in which both mates incubate eggs, brood small chicks, and feed them until they fledge (Boersma et al. 1990). They breed in nests dug in the soil or under bushes, and having a poor quality nest reduces fitness (Stokes and Boersma 1998). Female Magellanic Penguins are seen at the colony less frequently than males and thus we expected nest acquisition to be less competitive for females than for males. We expected that the strategy "owners win" should have a higher chance of being evolutionarily stable in female than in male Magellanic Penguins because the cost of losing is less for females. Our study (1) examined why females fight; (2) compared the fighting behavior of females with males; and

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(3) determined whether body size, physical condition, or ownership predicted who won female fights.

METHODS

The largest breeding colony of Magellanic Penguins is located at Punta Tombo, Argentina (44° 02′ S, 65° 11′ W). From September 1992 through January 1996 we watched for fighting penguins in a study area within the colony that was mainly devoid of vegetation and had a density of 20–30 nests/100 m^2 (Stokes and Boersma 2000).

We watched during most of the four breeding seasons approximately 2,000 nests for a total of 463 h. We observed primarily during the early morning and late afternoon, when penguins were most active (Renison et al. 2002). A fight was considered to start when two birds mutually pecked or flipper hit each other, and ended when contestants lost contact for ≥5 min. We recorded fight duration and counted the total number of flipper hits (we were unable to differentiate who received and who gave flipper hits). The sum of the length of cuts on each opponent was measured to the nearest mm.

After a fight, we marked the contested nest, captured both contestants, and banded them with stainless steel flipper bands. We measured bill length and depth, and flipper and foot length (see Boersma 1974). We determined the sex of fighters by body measurements (Scolaro et al. 1983), patterns of pairing and arrival to the colony (Boersma et al. 1990), and visual examination of their cloacas (Boersma and Davies 1987).

We systematically visited all nests in the study area to find females once in early October when most birds were in the colony, and in mid-October when females were incubating. In addition, we searched for contestants by walking around the area for ≥20 min every 2–8 days from September through mid-February. We may have missed some females that lost their eggs early, but females that fledged chicks were likely to be found.

We marked nests with female contestants and visited them every 4–15 days during the breeding season to determine nest contents. We measured the length and width of the eggs and we calculated an egg volume index by multiplying length by $width^2$. Chicks were individually marked and were considered to have fledged if they were alive after January 8 and their mass was ≥1.8 kg (Boersma et al. 1990). We considered a female the parent of the eggs or chicks in the nest when it was the only female present at the nest 6 days before the eggs were laid or if the male and female were seen consistently at the nest after egg laying.

We determined if females fought for the best quality nests by comparing nest quality codes where fights occurred with a comparison nest. Comparison nests were chosen as the closest nest with no eggs or chicks, occupied by a female with no cuts or blood that was not seen fighting during that season. The nest quality score ranged from "1" (poorest, nests which consisted of a scrape with no roof cover) through "5" (best, nests well covered; see Stokes and Boersma 1998, Renison et al. 2002).

The benefits of winning a fight can be measured as the increase in fitness as a result of winning (Grafen 1987). We quantified the benefits of winning by comparing between winners and losers three variables related to fitness: nest ownership, nest quality, and number of chicks fledged. If fighting ability and parental quality were positively associated, this would confound results as higher reproductive success would not necessarily result from winning. We determined whether fighting ability and parental quality were associated by comparing breeding success of winners and losers that had nests of similar quality, and by comparing egg volume of winners and losers. Egg volume is a good predictor of female parental quality (Reid and Boersma 1990).

For comparison of fight characteristics between sexes we chose 23 male-male and 23 female-female fights that were of similar duration (≤5 s) and which were matched for nest quality and date (≤4 days). To determine if size, body condition, and ownership were important for winning fights we calculated a body size index as the first factor extracted from a principal component analysis of body measurements. We calculated a body condition index as the standardized residuals from the linear regression of the first factor extracted from a principal component analysis of body measurements and body weight (Yorio

and Boersma 1994, Hood 1996). A female was classified as the nest owner if it was the parent of the eggs laid in the nest during the previous breeding season.

For statistical analysis we pooled data for all seasons. Fight duration (ANOVA: $F = 0.41$, df = 3, $P = 0.75$), length of cuts (Kruskal Wallis ANOVA: $\chi^2 = 2.054$, df = 3, $P = 0.56$), body size ($F = 0.96$, df = 3, $P = 0.42$), and body condition ($F = 1.33$, df = 3, $P = 0.27$) were similar among seasons, and all results had similar trends when analyzed for each season separately. We used paired statistical comparisons (paired sign, Wilcoxon, and *t*-test) when comparing winners with losers, and contested with comparison control nests. We randomly deleted fights where individuals or nests were sampled more than once (8 out of 55 fights). Complete information did not exist for all fights so sample sizes varied depending upon the test. For example, six fights had started by the time we arrived so fight duration was not known. We did not measure eggs of one or both contestants in 12 fights because eggs disappeared before we visited the nest or were never laid, and we knew nest ownership in the previous season for only 10 pairs of female opponents. Female-female fights were rare after the onset of incubation so we excluded the five fights we observed after the onset of incubation (October 20).

RESULTS

We observed 47 independent female-female fights. Females always fought over nests where a male and a female already were present. A female entered the nest site and began to vocalize at the female in the nest and tried to peck at her. Males did not peck or push the intruding female but often vocalized with one or both of the females. Most of the fights took place inside nests with females trying to push and bite each other. Fights lasted ≤56 min and eventually one female would leave the nest. On 36% of the occasions (17 of 47 fights) the female that left the nest re-entered the nest and continued to peck and push at the female in the nest. The male pecked at the losing female only when it was clear who the winner was.

Females fought from mid-September when they arrived at Punta Tombo. Female fights peaked during the first ten days of October at the start of egg laying (mean fights/h = 0.26 ± 0.08 SE). Females did not fight during incubation. A second small peak of fighting occurred after incubation for a 10-day period in mid-December (mean fights/h = 0.13 ± 0.07 SE), exclusively in nests without eggs or chicks.

Females fought in nests which were of better quality (mean nest quality score = 4.19 ± 0.13 SE) than comparison nests (mean score = 3.65 ± 0.13 SE; Wilcoxon paired test: $n = 47$, $Z = 3.66$, $P < 0.001$). Ninety-eight percent of the winners stayed in the contested nest while 85% of the losers moved to an alternative nest ($n = 47$ winners and losers; sign test: $P = 0.067$). Loser nests were of poorer quality than the nests for which they fought (mean nest quality scores: 4.37 ± 0.11 SE for winners, 3.43 ± 0.18 SE for losers; Wilcoxon paired test: $n = 47$, $Z = 3.66$, $P < 0.001$). Winners fledged more chicks (mean = 0.60 chicks ± 0.10 SE) than losers (mean = 0.31 chicks ± 0.08 SE; $n = 47$, $Z = 1.92$, $P = 0.047$). Winners and losers in nests of identical quality had similar reproductive success (winners fledged a mean of 0.47 chicks ± 0.17 SE, losers 0.53 chicks ± 0.19 SE; Wilcoxon paired test: $n = 15$, $Z = 0.22$, $P = 0.82$). Egg volume was similar between winners and losers (mean egg volume score for winners = 332.9 cm^3 ± 7.8 SE, mean for losers = 314.9 cm^3 ± 9.9 SE; paired *t*-test: $t_{34} = 1.33$, $P = 0.19$).

Female-female fights were less common than male-male fights (47 versus 138; $\chi^2 = 44.7$, df = 1, $P < 0.001$). Female-female fights were longer than male-male fights (Kolmogorov-Smirnov test: $Z = 2.97$, $P < 0.001$). When comparing female and male fights paired by fight length, nest quality, and date, we found that females received fewer flipper hits and shorter length of cuts than males (Table 1). Body size did not differ significantly between winners and losers (mean body size score for winners = 0.17 ± 0.25 SE, for losers = −0.07 ± 0.28 SE; paired *t*-test: $t_{46} = 1.18$, $P = 0.50$). Winners were in better physical condition than losers (mean body condition score for winners = 0.07 ± 0.05 SE, for losers = −0.02 ± 0.03; $t_{43} = 2.53$, $P = 0.008$). The difference in physical condition between opponents was not significantly correlated to fight length (Spearman correlation: $n = 41$, $r_s = 0.15$, $P = 0.36$). We knew the ownership

TABLE 1. During fights, female Magellanic Penguins received fewer hits and smaller cuts than males. Values are means ± SE.

	Females (n = 23)	Males (n = 23)	Wilcoxon paired test	
			Z	P
Flipper hits	1.39 ± 0.51	5.00 ± 1.76	2.045	0.039
Length of cuts (cm)	1.01 ± 0.21	3.98 ± 0.34	4.167	0.001

status of both contestants in 10 of the 47 fights. Nest owners won more fights (n = 8) than intruders (n = 2; binomial test: P = 0.055). Owners were in better physical condition in 9 of the 10 cases (binomial test: P = 0.011).

DISCUSSION

Female Magellanic Penguins fought over good quality nests during most of the breeding season, with two peaks of fighting: before and after egg laying. Fighting over nest sites or breeding territories before egg laying is well documented in penguins (Trivelpiece and Volkman 1979, Waas 1991) and other bird species such as male Purple Martins (*Progne subis*; Stutchbury 1991) and female European Starlings (*Sturnus vulgaris*; Sandell and Smith 1997). Because fights after egg laying were so few, we could not test why female Magellanic Penguins fought then even though they could not reproduce that season. However, in a related study in male Magellanic Penguins we found that fights after egg laying occurred mostly in nests without eggs or chicks which were of better quality than control nests, and male winners used the nest during the next breeding season (Renison et al. 2002). We believe that females also fight at the best nests after egg laying to establish ownership for the next breeding season. As males always were present at nests where females fought, females may be fighting for both a good quality nest and a good quality mate as well.

We found that on average female winners bred in higher quality nests and had higher reproductive success. Our results support the hypothesis that the difference in reproductive success between winners and losers could be due to the outcome of the fight (nest and mate acquisition) and not solely to preexisting differences in female quality. Egg size (an indicator of female quality; Reid and Boersma 1990) of winners and losers was similar, and when female opponents obtained nests of similar quality their reproductive success was similar. This suggests that winning makes a difference, and the quality of nests or mates may be the most important variables. Female physical condition before egg laying, however, is an important determinant of reproductive success (Yorio and Boersma 1994). Winners were in better physical condition than losers and therefore the difference in reproductive success between winners and losers probably also reflects the physical condition of the females.

Females were 9% less likely than males to return to our study area in the following year, suggesting that they may have lower survival or lower nest fidelity than males, and as a consequence there were more nests and mates available to females (Renison 2000). For fights before egg laying, 82% of the male winners and 40% of the male losers later were found breeding (Renison et al. 2002), while for females the percentages were 98% and 85%, indicating that females were more likely to find a nest or attract a mate. The relative benefits of winning a nest, therefore, were less for females than for males, and as predicted females fought less frequently and their fights were less intense than male-male fights. However, female–female fights were longer than male-male fights, perhaps because they were less intense. When females fought they pushed and pulled each other while inside the nest but were constrained by the burrow and could not use their flippers to hit their opponent. The total length of their cuts were shorter than when males fought.

Body condition and previous ownership of a nest predicted the outcome of female fights, while body size did not predict outcome. Body condition before egg laying may be important because females take the first incubation shift and need to fast until the male returns. Hence, females in better body condition

are more likely to be successful breeders (Yorio and Boersma 1994). Ownership may be important, because penguins that switch nests or mates have lower reproductive success (Fowler 1993). Hence, it is possible that body condition and ownership were good predictors of outcome *per se* or because they were associated to an asymmetry in resource value and females which were more likely to be successful breeders were more motivated to win.

In females, body condition, ownership, mate fidelity, and winning were strongly associated, suggesting that females may win because of all or some combination of these factors. We could not test which variable was the ultimate cause of female winning because they were strongly associated and we could not test them separately. However, if body condition *per se* is important in winning fights, when differences in body condition between contestants are small, fight duration should increase (Parker 1974, Enquist and Leimar 1983), which did not occur. The rule "owners win" is predicted to be an ESS only when benefits of winning are low, which did not appear to be the case for female Magellanic Penguins as winners fledged more chicks. This leaves us with the "asymmetry in resource value" hypothesis explaining who wins female fights. Differences in resource value between owners and intruders have been documented in Pied Wagtails (*Motacilla alba*; Davies 1981). Consistent with this interpretation, the male Magellanic Penguins did not interfere in the fights until the outcome was clear. They are likely to benefit by having a female which is in better body condition. Female fights may be longer not only because their fights are less damaging, but also because intruders need to be sure owners are highly motivated and can not be easily repelled.

We conclude that fighting in female Magellanic Penguins is less frequent than in males probably because females have less to lose by being expelled from a nest. Nevertheless, there is a cost. The small increase in reproductive success of females holding higher quality nests ensure that females, like males, will fight for high quality nests. Body condition and ownership were good predictors of winning, possibly because females in better body condition and which had bred in the nest the previous season are more motivated as nests are more valuable to them.

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SPRING MIGRATION AND STOPOVER ECOLOGY OF COMMON YELLOWTHROATS ON APPLEDORE ISLAND, MAINE

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ABSTRACT.—Although Common Yellowthroats (*Geothlypis trichas*) are Nearctic-Neotropical migrants that are common breeders across the United States and Canada, very little has been published about the migration and stopover ecology of this species. We used spring migration banding records of Common Yellowthroats from 1992–2001 on Appledore Island, Maine, to investigate potential sexual and age-related differences in migration timing and stopover ecology of this species. Arrival dates of males were significantly earlier than arrival dates of females during spring, with mean male arrival five days earlier than female arrival. Also, after-second-year (ASY) birds arrived significantly earlier than second-year (SY) birds within each sex. Males also were significantly heavier than females upon arrival on Appledore. During spring migration, 5.0% of males and 4.2% of females were recaptured at least one day after initial capture, resulting in a mean stopover length of approximately three days for both sexes. We found no significant difference in the mean minimum stopover length nor the rate of mass change between the sexes based on recaptured individuals. Furthermore, we found no significant differences in stopover ecology between age groups within either sex. Both sexes significantly increased mass during stopover, both as calculated from recaptured individuals and as estimated by regression of condition (mass × 100/wing chord) over time. Results of this study confirmed differential migration among Common Yellowthroats, which is consistent with previous studies of passerine migration ecology. Lack of differences in stopover ecology between the sexes or between age groups suggests that earlier arrival of males than females and of ASY birds than SY birds may be due to an earlier onset of migration rather than increased migration speed.
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Stopover sites provide locations for migrants to rest and forage to replenish energy stores during migration (Biebach et al. 1986, Bairlein 1987, Moore and Kerlinger 1987, Winker et al. 1992a, Morris et al. 1996). Several factors may determine the length of stopover, including timing of migration (Alerstam and Lindström 1990, Lavee et al. 1991), condition of migrants upon arrival (Moore and Kerlinger 1987), the availability of food (Kuenzi et al. 1991, Morris 1996), and competition (Francis and Cooke 1986, Moore and Yong 1991). If sufficient rewards are not obtained from foraging, migrants will either leave the stopover site in search of rewarding habitat (Kuenzi et al. 1991) or be forced to delay departure in order to obtain sufficient resources for the continuation of migration (Moore and Kerlinger 1987). Authors recently have discussed the importance of stopover sites for the conservation of long distance migrants (Berthold and Terrill 1991, Moore and Simons 1992, Moore et al. 1995).

Previous research has shown that for most wood warblers (family Parulidae), males migrate earlier than females during spring (Francis and Cooke 1986, Moore et al. 1990, Yong et al. 1998). Information on arrival dates and stopover lengths along the migration route allows a comparison of the timing of migration between the sexes. Furthermore, because time spent at stopover sites increases the total time of migration, birds that are time limited might be expected to decrease the time spent at stopover sites. Thus, one might predict that males would be less likely to be recaptured and would stay at stopover sites for a shorter period of time than females.

The Common Yellowthroat (*Geothlypis trichas*) is a common summer resident in marshes and shrub habitats in much of North America (Guzy and Ritchison 1999). During spring, Common Yellowthroats migrate from their wintering grounds in the southern United States, Central America, and the Caribbean to their breeding grounds throughout the United States and southern Canada (Rappole et al. 1995, American Ornithologists' Union 1998). Relatively little research has been published

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TABLE 1. Common Yellowthroats were common spring migrants on Appledore Island, Maine, from 1992 to 2001. Although the ranges of capture dates often overlapped, males were captured earlier than females in each year of the study. Annual capture effort is provided for comparison.

Year	Dates of operation	Total Net-hours[a]	Individuals captured	Range of capture dates (mean)	
				Males	Females
1992	2 May–31 May	2,428	581	11 May–1 June (23 May ± 5.4)	11 May–1 June (26 May ± 4.0)
1993	8 May–5 June	2,407	661	9 May–2 June (17 May ± 5.3)	11 May–3 June (22 May ± 6.1)
1994	30 April–4 June	3,461	599	4 May–1 June (20 May ± 6.3)	10 May–4 June (25 May ± 3.9)
1995	30 April–8 June	4,550	665	10 May–6 June (20 May ± 3.7)	17 May–8 June (24 May ± 4.1)
1996	6 May–8 June	3,504	359	7 May–9 June (17 May ± 4.7)	12 May–8 June (25 May ± 7.6)
1997	6 May–9 June	3,382	495	11 May–9 June (20 May ± 6.0)	12 May–9 June (26 May ± 5.1)
1998	7 May–9 June	3,929	793	8 May–7 June (21 May ± 4.7)	8 May–7 June (25 May ± 4.6)
1999	6 May–10 June	4,107	533	9 May–8 June (21 May ± 6.0)	12 May–8 June (26 May ± 4.5)
2000	4 May–10 June	4,093	283	4 May–9 June (16 May ± 7.0)	9 May–9 June (22 May ± 7.3)
2001	3 May–11 June	4,494	465	3 May–9 June (22 May ± 7.8)	9 May–10 June (29 May ± 5.1)

[a] Net-hours are a unit of effort equal to one 12-m net open for 1 h.

on migratory patterns of the Common Yellowthroat prior to the present study (Guzy and Ritchison 1999, but see Francis and Cooke 1986, Woodrey and Chandler 1997).

This study used banding data to document the migration and stopover ecology of Common Yellowthroats on Appledore Island, Maine. Although many warbler species use Appledore Island as a stopover site (Morris et al. 1994, 1996), the Common Yellowthroat is one of the few species of warblers that breeds at that site (Borror and Holmes 1990). Because they regularly have bred on the island, Common Yellowthroats are likely to find Appledore Island to be a high quality stopover site. We investigated the timing of arrival, stopover ecology, and change in mass during stopover of the Common Yellowthroat to examine differences in migration and stopover ecology between the sexes and between age groups. Our hypotheses were that (1) males would arrive earlier than females, (2) adults would arrive earlier than young birds within each sex, (3) males would be less likely to be recaptured and have shorter stopovers than females, (4) both males and females would gain mass during stopover, and (5) because females migrate later when food is more abundant, they would have greater mass gains than males.

STUDY AREA AND METHODS

Data collection.—The Appledore Island Migration Banding Station was operated during spring migration from 1992–2001 on Appledore Island, Maine. Appledore Island (42° 58′ N, 70° 37′ W) is the largest island in the Isles of Shoals, is dominated by shrubby vegetation, and is approximately 10 km southeast of Portsmouth, New Hampshire. Morris et al. (1994) provided a detailed description of the field site. The banding station generally opened during late April or early May and ran until early June (Table 1). We captured migrants in mist nets (up to 10 nets, 12 m long, 30 mm mesh) that were opened just prior to sunrise, closed just after sunset, and checked at least once every 30 min throughout the day. We took all birds captured to a central location for banding. For each bird captured and recaptured, we recorded band number, species, age, sex, wing chord (to 0.5 mm), tarsus length (to 0.1 mm), fat class (0–4), and mass (to 0.01 g). We determined the age of yellowthroats according to the U.S. Fish and Wildlife Service (1977), Wood and Beimborn (1981), Pyle et al. (1987), and Pyle (1997). We did not assign yellowthroats to second-year (SY) and after-second-year (ASY) categories regularly until 1998.

Although Common Yellowthroats regularly breed on Appledore Island (Borror and Holmes 1990), most of the individuals captured likely were migrants for several reasons. First, the number of individuals captured each spring was at least an order of magnitude greater than the number of breeding pairs on the island, estimated by Borror (1995) at nine pairs (Table 1). Second, few individuals were recaptured during subsequent seasons or

years. To reduce the likelihood of including residents, any bird that was captured during a subsequent banding season (e.g., the subsequent fall or the following spring) was considered to be a resident and was excluded from the analyses of stopover patterns.

Data analysis.—We created two condition variables to give scaled indices of body mass. The condition index was calculated as mass × 100/wing chord (following Winker 1995). Because wing chord varies with age as well as with overall size and sex (Pyle et al. 1987, Pyle 1997), we also created an alternative condition index, calculated as mass × 100/tarsus.

We calculated stopover length by subtracting the initial capture date from the date of final recapture. This value is the minimum time a bird spent on Appledore because we could not assume that we captured an individual on its first day on the island nor could we assume that final recapture occurred on its last day on the island (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). We calculated relative mass change for each individual recaptured at least one day after initial capture by using the following formula (final mass − initial mass)/initial mass. To account for potential differences based on the length of time a migrant stayed at the site, we also calculated daily relative mass change as relative mass change/minimum stopover length. We did not include birds captured later during the same day they were banded in analyses of mass changes to avoid handling effects (Schwilch and Jenni 2001). We also used simple linear regression to investigate the relationship between condition index (described above) and time of capture for all individuals captured (Winker et al. 1992a, 1992b; Winker 1995).

We performed all statistical analyses using SYSTAT 9.0 (SPSS, Inc. 1998). Differences between sexes in the timing of migration and initial mass were investigated using two-way ANOVAs that included year as a factor. We also performed these analyses to investigate all four age-sex categories simultaneously. To investigate the relationship of body condition with arrival date, we regressed both condition indices over time. After verifying no significant variation among years, we pooled data for stopover variables across years. We used likelihood ratio chi-squared analyses to test for differences in recaptures between males and females. We used paired *t*-tests to investigate mass change among recaptured individuals. We investigated differences between sexes in stopover lengths and mass gains among recaptured individuals using two-sample *t*-tests, assuming unequal variance. We also calculated mass gains by regressing condition over time of capture (h after sunrise) following Winker (1995) and Dunn (2000). Differences between sexes were tested for significance using ANCOVA analyses after verifying that interactions between time and sex were not significant. All *P* values from statistical analyses tests reflect two-tailed tests. Whenever tests were performed on individual years, we used a sequential Bonferroni procedure to correct for multiple tests (Rice 1989, Beal and Khamis 1991).

RESULTS

We captured a total of 5,378 Common Yellowthroats during spring migration from 1992–2001 (Table 1). The Common Yellowthroat was the most common migrant captured on Appledore during spring, accounting for a mean of 20.6% ± 4.9 SD of the individuals captured each spring. The range of capture dates was 3 May through 10 June for males and 8 May through 10 June for females (Tables 1 and 2). Males arrived significantly earlier than females ($F_{1,5358} = 116.4$, $P < 0.001$). Arrival dates differed significantly across the ten years of this study ($F_{9,5358} = 66.1$, $P < 0.001$), and males arrived before females during each of the 10 years ($P < 0.001$; Table 1). The mean arrival date of males was 5 days earlier than females (Table 2). Timing of migration varied significantly among age and sex categories, with ASY birds arriving earlier than SY birds ($F_{3,1835} = 216.4$, $P < 0.001$; Fig. 1), and this pattern held for each of the four years in which we regularly assigned individuals to all four age categories ($P < 0.001$). Males were significantly heavier than females upon arrival ($F_{1,5318} = 120.5$, $P < 0.001$; Table 2), and although mass varied significantly across years ($F_{9,5318} = 16.4$, $P < 0.001$); the same pattern held for each of the ten years of this study ($P < 0.001$).

Regression of wing chord by date of arrival indicated that individuals with longer wing chords tended to arrive earlier than individuals

TABLE 2. Although male Common Yellowthroats arrived earlier than females, males and females used Appledore Island, Maine, similarly as a stopover site during spring migration (data from 1992 to 2001 was pooled). Capture dates, mean wing chord, and initial mass include data from residents. Recapture rate, stopover length, and mass change refer to data from migrants only. Means are presented with standard deviations.

Variable	Males	Females
Number of individuals captured	2,773	2,605
Range of capture dates	3 May–10 June	8 May–10 June
Mean date of capture (days)	20 May ± 6.0	25 May ± 5.4
Mean wing chord (mm)	53.8 ± 1.6	50.7 ± 1.4
Mean initial mass (g)	10.44 ± 0.80	9.67 ± 0.73
Mean recapture rate (%)[a]	5.2 ± 2.8	4.3 ± 1.2
Mean stopover length (days)	3.2 ± 2.5	3.6 ± 2.8
Mean mass change (g)	0.21 ± 0.80	0.30 ± 0.82
Mean mass change (%)	2.34 ± 8.10	3.45 ± 8.65
Mean rate of mass change (g/h)[b]	0.012 ± 0.004	0.029 ± 0.004

[a] Mean recapture rate refers to mean annual recapture rate.
[b] Rate of mass change was calculated using regression coefficients of condition (mass × 100/wing chord) over time of capture and mean wing chord.

with shorter wing chords among both males and females (males: $F_{1,2771} = 215.5$, $P < 0.001$; females: $F_{1,2602} = 113.5$, $P < 0.001$). Regression of tarsus length on date of arrival indicated that there was no significant effect for either sex (males: $F_{1,2770} = 1.3$, $P = 0.25$; females: $F_{1,2601} = 0.3$, $P = 0.60$). The regression of condition index (based on wing chord) on arrival date indicated that for both sexes, relatively heavier individuals arrived earlier than lighter individuals (males: $F_{1,2751} = 67.0$, $P < 0.001$; females: $F_{1,2583} = 96.0$, $P < 0.001$). A similar regression of alternative condition index (based on tarsus length) on arrival date also found significant correlation between higher condition and earlier arrival (males: $F_{1,2751} = 4.6$, $P < 0.05$; females: $F_{1,2582} = 35.9$, $P < 0.001$).

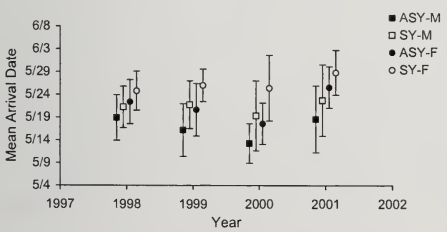

FIG. 1. Arrival dates of male Common Yellowthroats were significantly earlier than arrival dates of females during spring on Appledore Island, Maine, from 1998–2001. Also, after-second-year (ASY) birds arrived significantly earlier than second-year (SY) birds within each sex. Sample sizes are as follows. 1998: ASY-M, $n = 82$; SY-M, $n = 213$; ASY-F, $n = 66$; SY-F, $n = 291$. 1999: ASY-M, $n = 85$; SY-M, $n = 175$; ASY-F, $n = 37$; SY-F, $n = 207$. 2000: ASY-M, $n = 64$; SY-M, $n = 81$; ASY-F, $n = 49$; SY-F, $n = 71$. 2001: ASY-M, $n = 58$; SY-M, $n = 152$; ASY-F, $n = 26$; SY-F, $n = 182$.

Both sexes had a similar recapture rate. Among males 5.0% (138 of 2,773) of individuals and among females 4.2% (110 of 2,605) of individuals were recaptured at least one day after their initial capture ($\chi^2_1 = 1.7$, $P = 0.19$; Table 2). Recapture rates were similar between the sexes during each year of the study except during 1997, when males were significantly more likely to be recaptured than females ($\chi^2_1 = 9.7$, $P < 0.01$). We did not find a significant difference in recapture rate between age groups in either sex (males: $\chi^2_1 = 2.0$, $P = 0.16$; females: $\chi^2_1 = 1.1$, $P = 0.30$). There was not a significant difference in stopover length between the sexes ($t_{222.5} = 1.15$, $P = 0.25$; Table 2), between age categories within a sex (males: $t_{14.9} = 0.46$, $P = 0.66$; females: $t_{3.4} = 0.9$, $P = 0.41$), or among years in males ($F_{9,128} = 1.07$, $P = 0.39$; Table 3), although females did differ significantly among years ($F_{9,100} = 2.62$, $P < 0.01$; Table 3). Regression of capture date on length of stay indicated no relationship between arrival date and amount of time spent on Appledore in either sex (males: $F_{1,136} = 1.32$, $P = 0.25$; females: $F_{1,108} = 0.26$, $P = 0.61$).

Mean mass gains indicated that recaptured birds of both sexes increased their mass significantly during stopover (males: $t_{134} = 3.37$, $P < 0.001$; females: $t_{107} = 4.14$, $P < 0.001$; Table 2), although some individuals did lose

TABLE 3. Male and female Common Yellowthroats showed slight annual variation and little difference between the sexes in stopover ecology on Appledore Island, Maine, from 1992 to 2001. Means are presented with standard deviations.

	Males			
Year	Percent recaptured (*n*)	Stopover length in days (*n*)	Mass change (% of initial mass)	Rate of mass change[a] (g/h)
1992	3.0 (338)	2.0 ± 1.3 (10)	2.3 ± 7.9	0.016 ± 0.010
1993	3.4 (350)	3.4 ± 2.4 (11)	8.4 ± 8.8	−0.033 ± 0.011
1994	6.3 (284)	3.1 ± 2.1 (18)	−0.6 ± 5.9	0.030 ± 0.012
1995	4.0 (326)	2.5 ± 2.6 (13)	2.5 ± 8.4	0.025 ± 0.010
1996	4.4 (203)	2.4 ± 1.6 (9)	1.2 ± 6.2	−0.011 ± 0.015
1997	11.4 (219)	3.8 ± 2.6 (25)	2.3 ± 9.3	0.011 ± 0.012
1998	5.9 (376)	3.6 ± 3.6 (22)	2.3 ± 7.4	0.022 ± 0.009
1999	3.3 (274)	2.4 ± 1.2 (9)	−0.3 ± 4.9	0.046 ± 0.013
2000	7.7 (156)	4.3 ± 2.2 (12)	4.6 ± 8.7	0.001 ± 0.020
2001	4.9 (243)	3.6 ± 3.0 (5)	6.0 ± 9.7	0.026 ± 0.017

[a] Rate of mass change was calculated using regression coefficients of condition (mass × 100/wing chord) over time of capture and mean wing chord.

mass at the site. Among these recaptured birds, males and females did not differ significantly in their relative mass change during stopover ($t_{222.1} = 1.02$, $P = 0.31$), nor did they differ significantly in their daily relative mass change during stopover ($t_{230.5} = 0.87$, $P = 0.39$). Within each sex, there was no significant difference in mass gain or rate of mass gain between age categories. Relative mass change for both sexes was significantly correlated with length of stay, with individuals that stayed longer gaining more mass (males: $F_{1,132} = 45.8$, $P < 0.001$; females: $F_{1,107} = 11.3$, $P = < 0.01$; Fig. 2).

Positive slopes of regression of condition over time of capture indicated that Common Yellowthroats were gaining mass on Appledore Island and that this gain was significantly different between sexes (mass gain: $F_{1,5332} = 56.9$, $P < 0.001$; sex: $F_{1,5332} = 77.3$, $P < 0.001$). Both males and females experienced significant mass gains as estimated by regression of condition over time of capture (males: $F_{1,2732} = 10.1$, $P < 0.01$; females: $F_{1,2573} = 55.0$, $P < 0.001$), although variation among years also was significant (males: $F_{9,2732} = 4.6$, $P < 0.001$; females: $F_{9,2573} = 12.2$, $P < 0.001$). We also found a significant difference among the four age and sex categories in mass gain as estimated by regression of condition over time of capture ($F_{3,1823} = 11.7$, $P < 0.001$). This difference occurred in three of the four years during which most birds were assigned to a specific age category (1998: $P < 0.001$; 1999: $P < 0.01$; 2000: $P < 0.001$), but during 2001 the same pattern did not hold ($P = 0.12$).

DISCUSSION

The mean arrival of Common Yellowthroats on Appledore Island (May 22) was approximately 10 days later than the mean arrival at Powdermill Nature Reserve, Pennsylvania (Rotenberry and Chandler 1999). A striking feature of Common Yellowthroat migration on Appledore Island was differential migration as evidenced by the earlier arrival of males than females at this stopover site during spring. These results corresponded to results of other studies of Neotropical migrants. Moore et al. (1990) reported earlier arrival dates of male passerines on a stopover island after spring trans-Gulf migration and suggested an earlier departure of males from wintering grounds rather than a differential rate of migration to explain the observed difference between the sexes. Francis and Cooke (1986) reported a mean arrival date for Common Yellowthroats of 19 May for males and 23 May for females at a banding site in the Great Lakes region positioned 1° north of Appledore Island. Our reported 5-day difference in arrival dates between the sexes was similar to their findings, although arrival dates on Appledore Island were two days later than the arrival dates that Francis and Cooke reported.

Several hypotheses have been proposed to suggest reasons why it may be advantageous to arrive early at the breeding grounds, where males are likely to encounter intrasexual com-

TABLE 3. EXTENDED

Females			
Percent recaptured (*n*)	Stopover length in days (*n*)	Mass change (% of initial mass)	Rate of mass change[a] (g/h)
3.3 (236)	1.8 ± 1.4 (8)	2.4 ± 7.4	0.017 ± 0.010
3.4 (297)	3.4 ± 1.9 (10)	2.8 ± 6.6	0.037 ± 0.013
5.6 (302)	2.6 ± 1.3 (17)	1.2 ± 4.9	0.029 ± 0.010
5.8 (326)	3.7 ± 3.0 (19)	3.7 ± 8.4	0.025 ± 0.010
4.1 (148)	3.0 ± 2.5 (6)	7.5 ± 10.1	0.024 ± 0.016
4.1 (272)	6.1 ± 4.6 (11)	4.5 ± 8.4	0.006 ± 0.010
3.4 (416)	3.0 ± 2.8 (14)	1.7 ± 10.4	0.025 ± 0.009
3.9 (258)	2.8 ± 2.7 (10)	0.5 ± 12.9	0.032 ± 0.012
6.3 (127)	4.6 ± 2.1 (8)	6.8 ± 8.9	0.035 ± 0.019
2.7 (220)	5.7 ± 3.0 (6)	10.8 ± 5.9	0.050 ± 0.013

petition for territory and mates. Males may migrate earlier because they (1) winter farther north and have a shorter distance to travel, (2) proceed at a faster rate than females, or (3) initiate migration earlier than females (Chandler and Mulvihill 1990). There are both advantages and disadvantages for males arriving early at the breeding grounds. Early-arriving males may experience harsher weather conditions or lower food availability than males arriving later. However, early males may have a greater likelihood of establishing favorable territories (Lavee et al. 1991) and attracting mates since there are fewer competitors (Francis and Cooke 1986). Females may be at a greater disadvantage to arrive at the breeding grounds early, since their smaller size would be less suitable for severe weather (Ketterson and King 1977). In addition, females have less selective pressure to arrive early, since even a late-arriving female would likely find a mate, though possibly of lower quality, while a late-arriving male would likely not mate at all (Francis and Cooke 1986). Our finding that individuals captured earlier during the season had higher condition indices than later migrants may indicate that early migrants are prepared for potentially harsh weather conditions on the breeding grounds early during the season.

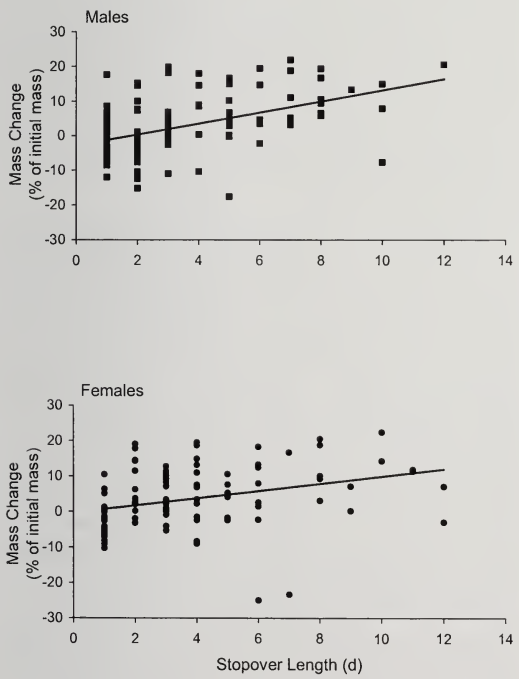

FIG. 2. Mass changes generally increased with length of stopover for recaptured male and female Common Yellowthroats on Appledore Island, Maine. Data from 1992–2001 were pooled for the regression analysis. For males, $n = 135$, $r^2 = 0.26$, and the equation for the regression line is $y = 1.62x - 2.85$. For females, $n = 108$, $r^2 = 0.11$, and the equation for the regression line is $y = 1.02 \times -0.25$.

Our results suggest that males may be initiating migration at an earlier date rather than proceeding at a faster rate than females. If males were to migrate at a faster rate, patterns of stay at stopover sites might vary between the sexes; however, results presented here indicate that there was no significant difference in recapture rate or stopover length between the sexes. Both males and females were re-

captured at the same rate and stayed on Appledore Island for the same length of time, suggesting that a differential rate of migration was not occurring. Our results differed from the results of a spring study of Wilson's Warblers (*Wilsonia pusilla*) in New Mexico in which males were less likely than females to be recaptured (Yong et al. 1998). However, our results for Common Yellowthroats were similar to findings by Morris and Glasgow (2001) for American Redstarts (*Setophaga ruticilla*) and the findings of Otahal (1995) for Wilson's Warblers in California, neither of which indicated a differential rate of recapture between the sexes.

Our finding that larger individuals of both sexes tended to arrive early on Appledore was consistent with results reported for Common Yellowthroats by Francis and Cooke (1986). The tendency for individuals with longer wing chords to arrive earlier may be attributed to either an age effect, a distribution effect (if larger birds were from northern populations), or both. Analyses of timing of migration relative to age indicated that ASY birds indeed were arriving earlier than SY birds in both sexes (Table 2, Fig. 1). However, to investigate the possibility that the observed relationship in arrival date and wing chord was related to size as well as age, we also performed regressions with tarsus length. This relationship was not significant among individuals of either sex. Since tarsus length does not increase with age, these results suggest that age, not simply size, was a factor in the arrival date in Common Yellowthroats, with SY birds arriving later than ASY birds in both males and females.

Moore and Kerlinger (1987) concluded that a stopover site was suitable if migrants gained mass during stopover, indicating that Appledore Island was a suitable stopover site for migrant Common Yellowthroats during spring. We found mean mass gains among recaptured males and females on Appledore, and we found that mean rates of mass gain were similar for both sexes, suggesting that both sexes utilized the stopover site to forage similarly. Therefore, it is not likely that males would require fewer stopovers to maintain energy reserves, which would lead to a faster rate of migration. Instead, both sexes obtained similar energetic gains during the same time period. In contrast, rates of mass gain as estimated by regressions of condition on time of capture indicated that males were gaining mass more slowly than females, potentially indicating an increased need for stopovers by males. The differences between the sexes in mass gains may indicate that there were greater food resources available to later migrants. In his study of the Wilson's Warbler, Otahal (1995) found that males and females gained the same mass during stopover. However, Yong et al. (1998) found that male Wilson's Warblers had a higher rate of mass gain than females during spring. This study found a positive relationship between length of stay and amount of mass gain, which indicated that Appledore Island apparently provided sufficient food rewards for stopover migrants, although the rate of mass gain was lower than two sites studied in southern Ontario (Dunn 2001). Winker et al. (1992a) also reported mass gain among Common Yellowthroats during spring at an inland stopover site in Minnesota, although several other species lost mass during spring at that site. It is interesting that Winker et al. (1992a) reported a mean stopover length of 3.3 days for Common Yellowthroats during spring at their site located 2° north of Appledore Island, which was similar to our findings.

The lack of difference in stopover ecology of recaptured individuals between males and females and between age groups in this study was similar to a recent study of American Redstarts on Appledore Island (Morris and Glasgow 2001). Similar work on Wilson's Warblers yielded contradictory results. Yong et al. (1998) reported increased recapture rates of females, increased rates of mass gain by males, and no difference in stopover length among age or sex groups in New Mexico. However, in California, Otahal (1995) found no difference in recapture rate or mass gain among males and females, although stopover length was significantly longer in males. Because these studies of stopover ecology of individual species have had different results related to sex, more study of potential sexual differences is warranted.

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REFLECTIONS ON A LIFETIME OF ORNITHOLOGICAL RESEARCH
The 2000 Margaret Morse Nice Lecture

SUSAN M. SMITH[1]

I still remember my excitement when, as a beginning graduate student, I first discovered the work by Margaret Morse Nice on Song Sparrows (*Melospiza melodia*). Her brilliant field research on color-banded Song Sparrows (Nice 1937, 1943) remains the standard of excellence for avian studies to this day. Certainly her work has continued to inspire me throughout my professional life. It is indeed a great privilege to have this chance to add my contribution to the series of papers in her honor.

BACKGROUND

I was born in Winnipeg, Manitoba. From a very early age, I was fascinated by living creatures. One day as I was walking to school, I saw a tiny bird, very close to me, in a hedge. My fifth-grade teacher happened to have a Peterson's field guide in the classroom, and I discovered that what I had seen had a name: it was a Golden-crowned Kinglet (*Regulus satrapa*). I was hooked for life.

My family moved frequently: from Winnipeg we moved to Saskatoon, Montreal, and finally to Vancouver, British Columbia, where I finished high school and then did my undergraduate work majoring in zoology at the Univ. of British Columbia. My honors thesis, done under the direction of M. D. F. Udvardy, was on niche differences between Chestnut-backed (*Poecile rufescens*) and Black-capped (*P. atricapilla*) chickadees and became my first published paper, in *The Wilson Bulletin* (Smith 1967a).

I stayed on at the Univ. of British Columbia to do a master's degree, working with Dennis Chitty on social behavior and survivorship in Black-capped Chickadees. This was my first color-banding project. Then I moved south of the border to do my Ph.D. at the Univ. of Washington with Gordon Orians. I may have been his first graduate student not to work on blackbirds; my dissertation was on the development of prey recognition and impaling behavior in young Loggerhead Shrikes (*Lanius ludovicianus*).

During my graduate studies at the Univ. of Washington, I took a field course in Costa Rica through the Organization for Tropical Studies during the summer of 1969. This was my first experience in the tropics, and it was an extremely important influence on my perception of the natural world.

Immediately after completing and defending my dissertation, I began teaching at Wellesley College. There I started a field study on color-banded Black-capped Chickadees, for the first time focusing in particular on their winter dominance hierarchies. Four years later I got married, and my husband Gary Stiles and I moved to Costa Rica. There I worked hard to improve my Spanish, then taught biology (in Spanish), first at the Univ. of Costa Rica in San Jose, and later at the National Univ. in Heredia. During the four years I lived in Costa Rica, I did research on a color-banded population of Rufous-collared Sparrows (*Zonotrichia capensis*) on the Univ. of Costa Rica campus, as well as hand-rearing work with both Turquoise-browed Motmots (*Eumomota superciliosa*) and Great Kiskadees (*Pitangus sulphuratus*).

My marriage did not work out, and I returned north in 1977 to teach briefly at Adelphi Univ. before moving on to Mount Holyoke College, where I settled in 1979, and where I still am today.

AREAS OF INTEREST

Most of my published work can be placed into one of three general topics, each of which is known to have interested Margaret Nice. The first two are strictly research: (1) the development of behavior, as addressed by hand-rearing studies; and (2) the social behavior of

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free-living birds, as addressed by color-banding studies. The third topic is more general and can be described as the importance of studying bird behavior without preconceived biases about the roles of males and females.

ONTOGENY EXPERIMENTS

In her landmark study on behavioral development in Song Sparrows, Margaret Nice (1943) obtained extensive data not only on hand-reared birds, but also on young sparrows in the wild. I based the experimental design for my work with Loggerhead Shrikes on her example (Smith 1972, 1973a).

In the field, I checked eight shrike nests daily, looking at the behavior of both adults and nestlings. After the young had fledged, I followed two family groups (totaling 13 young birds) until the young dispersed naturally. I then hand reared more than 60 young shrikes, with the developmental data on free-living shrikes as a baseline for comparison.

Ontogeny of impaling in shrikes.—Shrikes of the genus *Lanius* are well known for impaling their prey, and I was particularly interested in how such behavior developed in young shrikes. As predatory passerines, shrikes lack talons to hold down their prey. Most predatory birds lacking talons are restricted to eating only prey small enough to be swallowed whole. However, impaling behavior serves the same function as talons, thus allowing shrikes to exploit larger prey. Here I use the term "impaling" broadly to include both the wedging of prey in forks of a branch, and the anchoring of prey on a sharp thorn.

Starting about 20 days after hatching, young shrikes began what I termed "dabbing" behavior, in which the birds would take food in their bills, turn, and touch the food to their perch. Approximately two days after the onset of dabbing, the birds began pulling the food along the perch toward their bodies; this I termed "dragging" behavior. Lorenz and von Saint Paul (1968) described very similar types of behavior in the development of impaling in three other *Lanius* species.

At first, dragging behavior was not directed toward suitable locations (thorns or forks). However, if such items were available, the birds gradually started directing their dragging more and more to appropriate places, until at last they became proficient at impaling prey (Smith 1972).

I raised some shrikes in the absence of any impaling device, with only smooth dowels for perches. Shrikes kept in such conditions until they were ≥75 days posthatching, and then given thorns and forks, failed to use these for impaling, even if they had been given the daily opportunity to observe older shrikes impaling and wedging prey on thorns and forks in an adjacent cage. Thus the shrikes must have personal experience with suitable impaling locations in order for the dragging movements to develop into normal impaling behavior. Moreover, this experience must occur within a certain period (some time between 20 and 70 days after hatching), so the process involved in learning the orientation component of impaling seems very much like some form of imprinting.

Factors directing predatory behavior in shrikes.—Young shrikes, once fledged, are very curious and peck, pounce on, and even attempt to carry a wide variety of objects in their environment (Miller 1931a, 1937; Cade 1962, 1967; Smith 1973a). Under natural conditions, they begin catching small invertebrate prey within days of leaving the nest, and gradually become more skilled as they attempt to capture an ever wider variety of suitable prey. When hand reared, shrikes that were given a sequence of small to large live food to catch developed the ability to handle mouse-sized prey about 10 days sooner than birds not given such experience. Nevertheless, by the age of 40 days posthatching, all shrikes were capable of killing a mouse by directing pecks to the back of its neck in the manner of adult wild shrikes, even when this was the first live prey ever encountered (Smith 1973a).

I was curious to learn what aspects of a large (mouse-sized) potential prey object would be used by naïve shrikes to direct their pecks along its length. I presented my birds with a series of 12 wooden models, including some shown in Figure 1. The first model was plain, with no added cues, although I had divided it lengthwise into thirds, using very faint pencil marks. As expected, the birds ignored my pencil marks. They did, however, direct significantly more than two-thirds of their pecks to the two end thirds of this plain model. This makes sense, because terrestrial

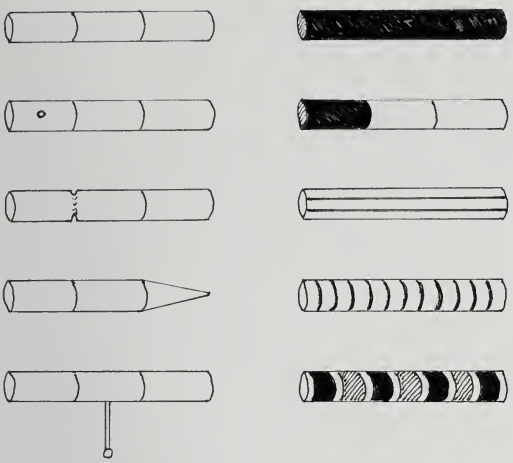

FIG. 1. Some sample models offered to hand-reared young birds. (Left) Unpainted models; from top: plain, eyespot, neck constriction, pointed tail, and plain moving model. Motion was achieved by inserting the nail into a slot in the floor of the cage. (Right) Painted models; from top: solid, end third, stripe pattern, ring pattern, and coral snake rings.

animals typically have their most vulnerable body parts near one end of their total body length.

The other 11 models all bore various cues singly or in combinations. These cues included eye spots, a "neck" indentation, and motion. When one of the end thirds differed from the other (by the addition of eye spots and/or neck), the birds all pecked significantly more at the different end. However, I found no evidence of heterogeneous summation; i.e., two or more of these cues did not elicit a consistently greater response than did just one of them. The shrikes may have been acting out of curiosity.

In contrast, motion, in and of itself, proved to be a powerfully directing cue. The shrikes gave a highly significant proportion of their pecks to the leading third of any moving model. A shrike would approach a moving model, follow it, then hop around to peck at the "head" end. As it would have been easier for the shrikes to follow a moving model and peck at the trailing end, this consistent strong response is clearly something other than just curiosity.

I also presented my shrikes with two mounted specimens of vertebrate prey: a Golden-crowned Kinglet and a deer mouse (*Peromyscus maniculatus*). Rather to my surprise at the time, the shrikes paid virtually no attention to the stuffed bird. In contrast, their responses to the stuffed mouse were intense, much more so than to any other item I offered to them. When the mouse was in the normal upright position, all of the shrikes (regardless of prior experience) directed their pecks to the back of its neck. However, if in their approach they blew the cotton-stuffed mouse over onto its side or back, they directed their pecks instead to small extremities: feet, nose, or tail. This in itself I found fascinating; simply changing the orientation of an object can have a profound influence on the responses it elicits.

Comparative studies.—Over the next few years, I hand reared young birds of several species possessing differing types of diet: Black-capped Chickadees, Gray Catbirds (*Dumatella carolinensis*), Blue Jays (*Cyanocitta cristata*), House Sparrows (*Passer domesticus*), and two Neotropical species, Turquoise-browed Motmots and Great Kiskadees. The first of these studies was conducted on hand-reared chickadees, catbirds, and jays. To my surprise, all three of these, soon after fledging age, performed behavior that was indistinguishable from the dabbing behavior of young shrikes. This behavior was least common in catbirds, and involved no lateral components. In both chickadees and jays, it was more persistent, and later developed a lateral component as well. However, in both chickadees and jays this was pushing away from the body, in contrast with the pulling movements (dragging) in shrikes (Table 1). Both chickadees and jays hoard food; presumably these movements relate to storing behavior. It is more difficult to suggest a possible reason for the dabbing of young catbirds (Smith 1973b).

I presented these young birds with models similar to those used for shrikes (Fig. 1), but scaled appropriately for the size of the birds. All seven species, regardless of size or diet, aimed significantly more than 67% of their pecks to the two end thirds of their plain wooden model; this ranged from a low of 79.0% for the Gray Catbirds to a high of 93.6% for the Blue Jays (Smith 1974a, 1976a, 1978a, 1980a). When one of the end thirds of a model was provided with some additional cue, such as an eyespot or a "neck" constric-

TABLE 1. Food manipulation in young passerines. Ages are days after hatching. Data from Smith (1973b, 1974a).

Species	Age at first dabbing	Age at first lateral movements	Type of lateral movements
Loggerhead Shrike	21	23	Pulling
Gray Catbird	12	—	—
Black-capped Chickadee	17	20	Pushing
Blue Jay	19	23	Pushing

tion (Fig. 1), all five of the species that received such models (chickadees, catbirds, jays, motmots, and kiskadees) directed the majority of their pecks at this different end. However, here again I found no consistent evidence for heterogeneous summation, so their responses may be explained simply by curiosity (Smith 1983).

An exception was the kiskadees' response to a model with one end sharpened into a "tail" (Fig. 1). Here the different third was the pointed end, but the kiskadees gave a highly significant response to the blunt end instead. Yet, it would seem to be easier for them to pick up the model by its point. Clearly, this response cannot be explained by curiosity; indeed, it suggests that kiskadees (which are known to eat lizards) may possess an innate recognition of "tail." Since many lizards can shed their tails when caught, a kiskadee attacking the blunt end of such prey would be able to eat the whole thing, whereas those attacking the more pointed end might well end up with just part of a tail (Smith 1978a). It is unfortunate that I did not offer this "tail" model to any other predatory species.

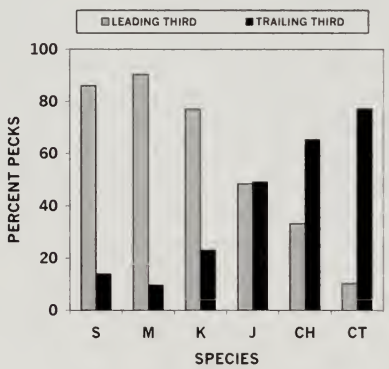

FIG. 2. Responses of six avian species to a plain moving model. The three predatory species, Loggerhead Shrike (S), Turquoise-browed Motmot (M), and Great Kiskadee (K) all responded significantly toward the leading third ("head") of the model. The omnivorous Blue Jay (J) pecked approximately the same at the leading and trailing thirds, while the two smaller species, Black-capped Chickadee (CH) and Gray Catbird (CT) pecked significantly more at the trailing third of the model.

Perhaps the most fascinating trend among the birds' behavior concerns their responses to motion. Figure 2 shows the responses of six species to plain moving models. The three predatory species (shrikes, motmots, and kiskadees) all responded by hopping around the moving model to direct their pecks at its leading third. Blue Jays gave virtually identical numbers of pecks at the front and hind end of this model. In contrast, the two nonpredatory species (as far as vertebrate prey is concerned) both gave a significant response to the trailing third of the model (Fig. 2).

Responses to colors and patterns.—Much of the work I did with colors and patterns was aimed at exploring mimicry systems through the behavior of potential predators. Most defensive mimicry systems (Batesian and Mullerian) function through predator learning (when a predator has a bad experience with a model) and predator generalization (when that predator generalizes to avoid attacking anything resembling that model; Wickler 1968, Morrell and Turner 1970).

However, the coral snake mimicry complex poses a different set of problems for would-be predators. True coral snakes have venom so lethal that any bad experience would result in death, and a dead predator cannot generalize to avoid anything at all. Given this problem, Wickler (1968) proposed that coral snakes are too lethal to serve as a model, and instead represent yet another type of defensive mimic, which he termed "Mertensian mim-

FIG. 3. Nestling Turquoise-browed Motmots, with eyes tightly shut.

ics." The actual models of this mimicry system then would be those snakes whose venom was sufficiently mild that a predator could survive being bitten, then proceed to avoid similar ring-patterned snakes. Certainly, Wickler said, there was no evidence that any predator could recognize coral snake patterns innately.

I decided to test this with Neotropical predators known to include small reptiles in their diet. The first species I used was the Turquoise-browed Motmot. This is a burrow-nesting species, and I obtained all of my nestlings before they had their eyes opened, so they had had no opportunity to see any colors or patterns other than what I gave them (Fig. 3).

I used four colors for the motmot experiments: yellow, red, light green, and dark blue, and presented these both as "solid" models, entirely covered with paint, and as "end-third" models, in which one end was painted, with the other two thirds being unpainted wood (Fig. 1). The motmots showed no hesitation in attacking solid models of each of these four colors, and directed most of their pecks at the painted third of the end-third models.

Then I began my pattern experiments. The first patterned model I presented to the motmots was a "solid" one, the entire model being covered with wide yellow and narrow red rings (Fig. 1). The response was impressive; every bird flew up to the opposite corner of the cage, and in many cases gave alarm calls. No bird directed any pecks at this model at all. The next model I made also was red and yellow, with the same proportions of the two colors, but this time the model had wide yellow and narrow red stripes, running the length of the model (Fig. 1). This the birds attacked with no hesitation. Finally, I made another ringed model, this time of wide light green and narrow dark blue rings. The motmots flew down and pecked this vigorously, directing their pecks particularly to the narrow dark blue rings.

When given end-third models with these patterns, the birds attacked all three, giving significant responses to the painted third of the red and yellow stripes and the blue and green

rings, but to the end farthest away from the red and yellow ringed pattern.

Clearly, therefore, the motmots were not afraid of a combination of red and yellow, since they attacked the striped model of those colors. Moreover, they were not afraid of a ring pattern itself, since they attacked the blue and green ringed model. However, when the rings were red and yellow, the birds showed a high degree of aversion. This I interpreted to be an innate response to a generalized coral snake pattern (Smith 1975).

My next experiments were on Great Kiskadees. These birds also have enclosed nests, so I could control the early experience of my birds with colors and patterns. Moreover, the geographical range of this species overlaps that of true coral snakes much more widely than does that of the motmots. This time I used five colors: red, yellow, black, dark green, and white.

The first pattern I had presented to the motmots was red and yellow rings, and so their negative response conceivably might have been due simply to novelty aversion (e.g., Coppinger 1970). Thus, after finding that the kiskadees readily attacked solid models of all five colors, the first pattern I gave them was wide white and narrow green rings. This they attacked with no hesitation. I could therefore conclude that neither novel patterns themselves, nor ring patterns in particular, were inherently frightening to these birds.

I gave two other ringed patterns to the kiskadees: red and yellow rings, and "coral snake" rings (wide red, narrow yellow, wide black, narrow yellow; see Fig. 1). No kiskadee approached either model. Nevertheless, the responses to the two differed; a few birds gave mild alarm calls to the former, while almost all of them gave high intensity alarm calls to the latter (Smith 1977).

Clearly, therefore, both of these potential predators have innate avoidance of patterns resembling coral snakes. Thus true, lethal, coral snakes can in fact serve as models in the mimicry complex, and the "Mertensian" mimicry hypothesis is unnecessary to explain the evolution and maintenance of this system.

Could this have been simply aversion to a generalized aposematic pattern? If so, then even birds that do not normally eat small reptiles, but often would encounter aposematically colored insects, might behave the same way. To test this, I hand reared Blue Jays and House Sparrows. I presented these birds with models painted a variety of color combinations: white and green rings; yellow and red rings; red and black rings; yellow and black "wasp" rings; black, white, and yellow rings in a monarch caterpillar pattern; and the red, yellow, and black coral snake ring pattern (Smith 1980a). The results were remarkable; all of the birds attacked every one of these models with no hesitation whatsoever (Fig. 4). Clearly, whatever made the kiskadees and motmots avoid red and yellow rings is not simply a universal aversion to warning coloration. Birds that normally do not encounter potentially lethal prey can afford to learn to avoid local aposematic patterns.

There are several lines of research one might follow based on some of this work. One involves a comparative approach. It would be interesting to choose a medium-sized omnivore that includes small reptiles in its diet. Perhaps there will be some populations that never encounter coral snakes, while other populations of this predator do overlap the coral snake range, either as residents or as migrants. One might predict that there would be a population difference in how hand-reared birds responded to coral snake patterns.

Coral snakes belong to the family Elapidae, and the diversity of this family in Australia is particularly high. At least some of the large Australian elapids have ringed patterns at an early age, which they lose later in life. Many Australian birds, such as some of the smaller kingfishers and perhaps members of the Cracticidae, are known to eat small reptiles. It would be interesting to see if such birds also had innate aversion to ringed patterns.

SOCIAL BEHAVIOR OF FREE-LIVING BIRDS

Behavioral ecology of floaters: (1) sparrows.—I first became interested in the behavior of floaters when I started color banding a population of Rufous-collared Sparrows on the Univ. of Costa Rica campus. This population had year-round breeding, and all the local suitable habitat was defended by resident, territorial pairs. To my temperate-trained eyes, the population was incredibly dense, although such densities are actually not at all uncom-

FIG. 4. Hand-reared young Blue Jay attacking a coral snake-ringed model.

mon in tropical regions (e.g., see Morton and Stutchbury 2000). Because of this high density, I had a lot of difficulty catching the sparrows. At first I tried mist nets. In no time I caught my first bird, and thought this would be easy. However, the territories were so small that the other birds could look down, see me putting up the nets, and then simply avoid them. It turned out the only way I was able to catch these birds was to set my nets before dawn so that they could not see where I was putting them.

My initial goal was to band all of the territory owners. This was not easy; if another bird entered the net in a given (small) territory at first light, the resident sparrows would watch as I extracted it, and then would avoid the net for the rest of the morning. So, when I caught unmarked sparrows, banded them, and discovered they were not members of the

resident pairs, I was at first bitterly disappointed. They were just floaters—what a waste of bands, which were not easy to obtain in Costa Rica at that time. I was sure I would never see these birds again.

But I did see them. When the first of my resident birds vanished, only to be replaced with a bird I had banded, in that very same (tiny) territory over two months previously, I was amazed. When it happened again, I began to realize that the floaters in my population clearly did not lead the sort of random, wandering existence usually assumed to be typical of floaters. So, I decided to focus my study on the social behavior of these birds.

I found that floaters tended to enter breeding territories most frequently in very early morning, then spend much of the rest of the day in a block of woods adjacent to my campus population that was unsuitable for sparrow breeding territories. Moreover, the marked floaters did not range evenly over my entire study area; instead, they had stable and highly restricted home ranges, being made up of just some of the breeding territories in the area.

Male floaters had home ranges encompassing 3–5 breeding territories. Interestingly, these were not necessarily contiguous. In contrast, female home ranges typically consisted of just one single breeding territory. The floaters of each sex had a consistent, well-defined dominance hierarchy for each of the territories within their home range. When an adult territory owner died, it was quickly replaced by the dominant local floater of the appropriate sex (Smith 1978b).

Twenty-eight of the more than 50 floaters I banded during the next three years (15 females and 13 males) succeeded in becoming territory owners within my study area. Thirteen of the 15 females, and 6 of the 13 males had been banded in the territory they later came to own. Of the remainder, the two females were banded a mean of 50 m away from their first territory, and the seven males a mean of 65.7 m away (Table 2). Several of these were within 10 m of the block of woods mentioned above, and the rest may well have been moving between the woods and their home range when I caught them.

I estimated that approximately half of the sparrows on my study area were floaters, yet a superficial glance at the area would detect primarily, and perhaps exclusively, the territory owners. I therefore termed these elusive floaters, with their highly organized social system, "the underworld" (Smith 1978b).

TABLE 2. Successful underworld Rufous-collared Sparrows. Data from Smith (1978b).

Sex and individual	Minimum time in the underworld (months)	Distance (m) between place marked and first territory
Females		
KWR	0.5	0
RG	0.5	0
OY	1.0	0
RRO	1.0	40
WR/WR	1.0	0
YRB	1.0	0
BY	2.0	0
YY	2.0	0
GHL	2.5	0
GK/GK	3.0	0
RYK	3.5	0
YB	3.5	0
GG	5.0	0
RB/RB	5.0	60
OO	8.0	0
Males		
BYG	0.5	0
YR2	1.5	0
RBO	2.5	60
RY/RY	2.5	50
WO/WO	2.5	80
YR	2.5	0
KK	3.0	0
OWK	3.0	100
1BG	5.0	120
RG/RG	7.0	10
RGW	7.0	40
RBO2	8.0	0
YB/YB	12.0	0

The only way for a young sparrow to obtain a breeding territory in suitable habitat, at least in my study area, was to join the underworld. Dispersing young birds that are still in striped juvenal plumage are more or less tolerated by adults, and can move about assessing where to set up their floater home ranges. Each bird presumably can assess the following four factors: territory quality, number of floaters of its sex already there, potential relations with its future mate, and health of the rival owner.

The relative importance of these four factors depends upon the gender of the floater. In my Costa Rican study area, Rufous-collared

Sparrows showed both year round breeding and year round female dominance. Perhaps as a result of this dominance, females can shift territories after having become an owner. Of my 10 records of owner territory shifts, only one was by a male; the other nine were by females. Probably most such shifts are to areas of higher quality.

This difference in dominance likely has strong effects on the relative importance of several of the four factors mentioned above. For males, who seldom shift territories after becoming owners, territory quality will be of very high importance; it is probably better for a young male to be relatively low ranked in the floater hierarchy of a high quality territory than to be more highly placed in a poorer quality territory. The relationship with future mates also is more important to males, since they are subordinate to females; this may explain the observed disjunct home ranges of male floaters.

For females, who can shift territories later more easily than males, starting rank likely is more important than territory quality, at least in fairly uniform habitat. Relations with future mates will be less important to females than to males, as resident males usually will not be able to reject them. Finally, health of the rival owner should be equally important to both male and female floaters (Smith 1978b).

There are several follow up studies I would love to see done. One interesting project on Rufous-collared Sparrows might be to work in an area of year round breeding, but with very marked variation in habitat quality. Under such circumstances there should be some territories with relatively large numbers of male floaters, while others might have few or even none (one would predict that female floaters would be more evenly distributed here). With the current technology allowing radio tracking of birds, determining floater home ranges and hierarchies should be considerably easier than it was when I first tackled it in the 1970s. Knowing where the floater hierarchies are longest might provide a "bird's eye view," as it were, for relative territory quality. One could compare male floater density with other factors more commonly used to estimate territory quality, such as availability of suitable nest sites, food, cover, or the like, to see which factors correlate most strongly with the birds' own choices. One also might predict that there could be certain lower quality territories where no male floaters occurred at all. It would be interesting to perform removal experiments on such territories to see if and from where any replacements came. If territories existed with no female floaters, those indeed would be inferior quality real estate.

Another interesting project would be to look at the social organization of underworld Rufous-collared Sparrows in more strongly seasonal, south temperate locations. Would the floaters there have such a highly organized system? When would this system form, and how long would it last?

Behavioral ecology of floaters: (2) chickadees.—When I arrived at Mount Holyoke College in the fall of 1979 and began color banding Black-capped Chickadees, I once again encountered floaters and, like the underworld sparrows, they also had restricted home ranges and well-defined dominance hierarchies. Floaters during the breeding season are well known; these are the birds capable of breeding but prevented from doing so by the behavior of others (Hensley and Cope 1951, Stewart and Aldrich 1951, Brown 1969, Smith 1978b). However, my chickadee study was conducted mostly during winter on nonbreeding flocks, and I was quite unprepared to find floaters at that time of year. There were indeed winter floaters, and in quite large numbers, too.

Most winter chickadees in my study area belong to a single home flock. These birds, which I termed "flock regulars," are organized into linear dominance hierarchies. The flocks, when first formed, contain equal numbers of males and females. Because the top-ranked male turns out to be paired with the top-ranked female, and so on down through the hierarchy, I suggested that a 10-bird flock (for example) actually functions as a hierarchy of five pairs (Smith 1988a, 1991).

Chickadee winter floaters have home ranges that include from 3–6 flock ranges. They typically move very rapidly between flocks; hence the term "flock switcher" (Smith 1984). I have found no gender-based difference in home range size of these birds.

Floaters initially ranked at the bottom of each of their flock hierarchies, below all regular members of their sex. However, given the opportunity, these birds could settle into one

of their flocks and assume a much higher rank. This was true for both male and female floaters. Such insertions always occurred after one of the regular members of a flock had vanished. Generally, only high-ranked openings were filled in this way; lower-ranked slots remained empty.

I observed two different kinds of floater insertion. In simple substitution, a high-ranked bird vanishes and is replaced by the highest ranked floater of the same sex, which pairs with the mate of the vanished bird; the ranks and pair bonds of the other members of the flock remain unchanged. Complex substitution involves two pairs within the flock. Here, if a member of the alpha pair disappears, two birds attempt to replace it: the top-ranked winter floater and a member of the beta pair. The latter succeeds in moving up, and the floater then inserts at the beta position (Smith 1984).

Floaters attempt to insert into only high-ranked slots in a flock; low-ranked slots stay unfilled all winter. Significantly, in most years only the top few pairs succeed in gaining local breeding territories; the lower ranked pairs typically are driven away at flock break up in the spring.

Having observed how this system worked under natural conditions, the next step was to conduct removal experiments. As I also was interested in long term survivorship in my study population, I obtained funding to build an aviary. Thus, when I removed a bird from its flock I could hold it in my aviary, observe the replacement process, then return the bird back into its flock and describe the subsequent social interactions (Smith 1987).

From November 1984 to January 1986, I performed 10 removal experiments. I decided to proceed under several restrictions. First, I removed birds only between November and February of any year to be sure that the flocks had fully formed in the fall and had not begun to break up in the spring. Birds were removed only from completely banded flocks. I removed each of the birds in the morning, to give it plenty of time to settle and discover food and roosting sites in the aviary well before nightfall. Finally, I took birds only when the weather was relatively warm, because they were held singly in the aviaries (Smith 1987).

Of the 10 birds removed, six (three females and three males) rapidly were replaced by floaters. All six of these birds were highly ranked in their flocks (Table 3). The other four birds (all males) were not replaced; all four of these were the lowest ranked birds of their sex in their flocks.

TABLE 3. Removal experiments on Black-capped Chickadees. Data from Smith (1987).

Removed bird	Flock size	Replaced?	Time (h) until first observed supplanting
#1 female	8	Yes	26
#1 female	4	Yes	5.5
#2 female	6	Yes	27
#1 male	4	Yes	30.25
#1 male	8	Yes	22
#2 male	4	No	
#3 male	6	No	
#3 male	6	No	
#4 male	8	No	

For all six high-ranked slots that I created in this way, the floater response was extremely rapid. One of the six insertions was by complex substitution, the other five by simple substitution. All six substitutions involved rapid and radical changes in dominance relations; settling birds began supplanting birds that, just hours before, had ranked well above them. Yet these major jumps in rank occurred literally overnight; the mean time between removal and first supplanting of the closest rival by the inserting floater was just 22.3 h. By the end of the second day, all the new ranks were firmly established.

No floater attempted to settle into any of the slots made by removing the four low-ranked males. This supports the field observations that low-ranked openings remain unfilled all winter.

I kept each of the captive birds in the aviary for four days, after which I released them back into their respective flocks. Upon release, all 10 birds regained their former rank immediately. They re-associated closely with their former mates, and lost no time in chasing away the floater that had briefly replaced them. The six floaters that had inserted then temporarily restricted their home range such as to avoid the flocks they had joined. Two of these six floaters later inserted into genuine openings and became local breeders the following spring (Smith 1987).

It turns out that I was fortunate to do these

removal experiments when I did them; soon afterward, the overall numbers of winter floaters in my study area dropped considerably, and thereafter, some high-ranked openings have remained unfilled, at least in certain years (Smith 1990). Nevertheless, I continue to have winter floaters in my study area, and have had at least some successful insertions (both simple and complex substitutions) in virtually every year so far.

Precisely what occurred to cause the marked drop in floater density in my study area is unclear. However, at approximately the same time, Tufted Titmouse (*Baeolophus bicolor*) numbers increased strongly in my study area. Whether or not the increased competition from this larger parid species had an impact on chickadee floater density is unknown.

Summer floaters (i.e., those during the breeding season) also occur in my chickadee population (Smith 1989, 1991). Perhaps the most interesting thing about these birds is that during 23 years of study every one I have seen so far has been present in the study area the previous winter. The vast majority (98%) of these birds were low-ranked regular members of a study area winter flock; the rest were winter floaters. Among chickadee summer floaters, male and female behavior usually is quite different. Male summer floaters are relatively easy to find; they often are quite vocal, concentrating their time in the less heavily used portions of local breeding territories. Female summer floaters are far more difficult to detect; they tend to be much more silent and skulking.

Whether or not territory owners will tolerate the presence of summer floaters probably depends upon local conditions that year. In my study area, summer floaters have occurred in only some years, and apparently are completely absent in others. When present, both male and female floaters can insert and replace a breeder of their sex; the absence of summer floaters in certain years is confirmed by the lack of replacements of breeders that vanish in May or June (Smith 1989).

Other aspects of population ecology and social behavior of chickadees.—My first field research project was on differences in foraging locations used by Black-capped and Chestnut-backed chickadees near the Univ. of British Columbia in Vancouver. I found that Chestnut-backed Chickadees foraged more in conifers, while Black-capped Chickadees foraged approximately the same amount in deciduous and in coniferous trees. There were height differences as well, with Chestnut-backed Chickadees feeding, on average, higher than Black-capped Chickadees. However this difference primarily reflected the fact that local conifers were much higher than deciduous trees; the mean distance from the top of the tree for each species was essentially the same (Smith 1967a). Most of my data were taken from mixed flocks, with records taken of both species each session. Looking at these paired records, one can see that the niche differences showed up consistently. Thus, the weather effects, later so well documented for parid foraging by Grubb (1975, 1977), probably did not have a major effect on my results.

My first color-banding study of Black-capped Chickadees also was conducted in Vancouver, British Columbia. There I looked primarily at changes in social behavior over time, and found that increased aggression associated with flock break up in the spring was correlated, in both years of the study, with a marked drop in overall chickadee density; all chickadees surviving this spring period obtained local breeding territories. I therefore concluded that the local breeding density of chickadees was regulated by territorial behavior (Smith 1967b).

The second location where I worked with color-banded chickadees was on the campus of Wellesley College in eastern Massachusetts. I was particularly interested to learn whether dominance hierarchies generated at feeders differed from those operating away from feeders. Although at the time I was disappointed that I detected no differences, I became grateful, as feeder-generated interactions tend to be more easily observed. I also hypothesized that in flocks containing more than one old (i.e., former breeder) male, the relative dominance between these birds might be affected by location. I thought that perhaps when a flock was near the nest site of one male, he would be dominant, but that this might shift when the flock entered the former breeding territory of the other male. Again my hypothesis was wrong; I found that my dominance hierarchies remained constant throughout each flock's entire home range (Smith

1976b). This study, which lasted four years, did support my third hypothesis, that alpha pairs would obtain better quality territories than would lower-ranked pairs. The alpha pairs' territories tended to be smaller in area, but with greater overall cover; they also had higher overall nestling feeding rates than did territories of lower-ranked pairs (Smith 1976b).

The rest of my work on chickadees involves my third population, in western Massachusetts. This ongoing study already has continued for more than twenty years.

As mentioned above, each Black-capped Chickadee winter flock is actually made up of a set of component pairs. I found, using the method of Ficken et al. (1981), that even members of pairs made up of two juvenile birds associated more closely with each other than with other members of their flock, and that this close association can be discerned in the fall, as well as later in the year (Smith 1990).

Pair bonds can persist for many years in chickadees (Odum 1942, Glase 1973, Smith 1991). However, they are not necessarily fixed for life. Thus, even when both members of a former pair are alive, one member can, under certain circumstances, desert the other and find a new mate. The first time I encountered this behavior was in my Wellesley population. An alpha male had a nest in an exposed metal pipe in a parking lot for at least two years in succession. The pipe would become very hot in the sun, and during incubation, his mate often could be seen panting at the nest entrance (in Black-capped Chickadees, females do all the incubation). The male had a different mate each year; even though both females survived the summer, they each joined another flock the following fall (Smith 1974b).

Divorce (the breaking of a former pair bond, where both members of the pair are still alive) can be initiated by both males and females. Although the Wellesley examples mentioned above appear to be a mode of escape from a difficult situation, most of my records can be thought of as a sort of social climbing. In 10 years of data from my current study population, there were 15 cases of divorce, while 79 other intact pairs (just over 84%) stayed together. Of the 15 divorces, 10 were initiated by females, and five by males. All 15 occurred after the death of another chickadee. Although these occurred both in the breeding and the nonbreeding season, I will treat the resulting changes in terms of the subsequent rank in the nonbreeding flocks. Fourteen of the records involved clear increases in rank. Each male initiator went from beta to alpha rank. Eight of the ten female initiators went from second- to top-ranked position, and one went from third-ranked to second-ranked position. The final record was slightly different; here a female that was top-ranked in a four-bird flock moved to become the top-ranked female in an eight-bird flock (Smith 1992).

In winter flocks, males rank higher than females. However, this gender-based dominance difference has no significant effect on overwinter survival; females survive the winter just as well as do males. Nevertheless, rank does have a significant effect on winter survival, but it is within-sex rank that matters, not between-sex rank. Thus, both members of a flock's high-ranked pairs survive significantly better than do members of lower-ranked pairs (Smith 1991, 1994).

Remarkably, at least in the first 10 years of my study, I found that significantly more young birds settled into my study flocks during falls preceding high winter survival, than in falls preceding lower winter survival (Fig. 5), suggesting that at some level chickadees during late summer or early fall, when the nonbreeding flocks are forming, can somehow assess conditions in the coming winter (Smith 1994). As yet I have not determined whether it is the older birds that assess the conditions and then regulate how many young birds to tolerate in the flocks as they form, and/or whether the young birds can detect these conditions and behave accordingly. Given the fact that many very different conditions could affect winter survival [food levels, involving both seed crops and possibly animal food as estimated (perhaps) by caterpillar damage on leaves; density and kind of predators and of their alternate prey species, to list just a few], this is not an easy question to resolve.

I have said that on average, females survive the winter just as well as do males. Nevertheless, male long term survivorship is somewhat higher than that of females (Smith 1994, 1995). The main time when the two curves diverge is when the birds are just over one

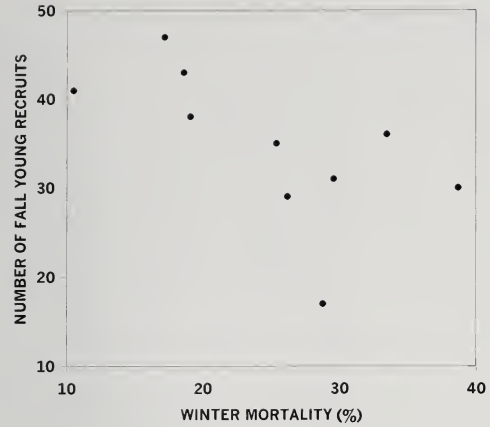

FIG. 5. Relationship between number of young Black-capped Chickadees settling into the nonbreeding flocks in the fall, and subsequent winter mortality in the study area. Significantly more young chickadees settled into the area before winters of low winter mortality; fewer settled before winters of higher mortality. From Smith (1994).

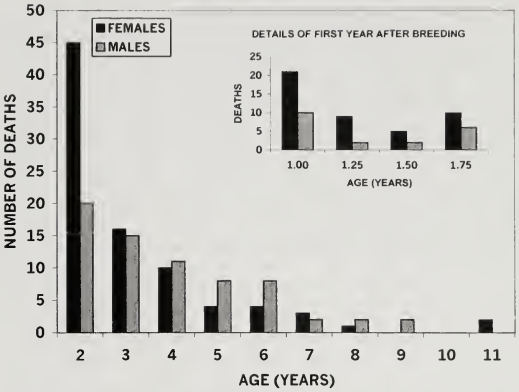

FIG. 6. Mortality of male and female Black-capped Chickadee breeders, starting with their second year of life (i.e., the first year after becoming breeders). Insert presents details of this critical year, separated into quarters: the first quarter ends on 30 June, the second 30 September, the third 31 December, and the fourth 31 March. Most of the difference between male and female mortality occurred during the first two quarters. Female mortality to the end of September (1.25 years) was significantly greater than male mortality during the same period. From Smith (1995).

year old, the end (for most of them) of their first breeding season and first postbreeding molt (Fig. 6). Males typically survive this period very well, but many females vanish at this time. I tried to see how those females who survived this period differed from those that did not. I found two factors that were significantly related to yearling female survival in late summer and early fall. One was previous winter rank; those with high initial rank survived their first full summer significantly better than those with lower initial rank in the previous winter flocks.

The second factor concerned the females' mates. Young females paired with older, experienced males survived the late summer period better than did young females paired with inexperienced males; this effect was particularly pronounced in years when the nighttime temperatures during incubation were relatively low. Inexperienced males in other species have been shown to be relatively inefficient in levels of courtship feeding (Lifjeld and Slagsvold 1986); this also may occur in chickadees. I concluded that young females given relatively little food support during incubation, especially in particularly cold years, may incur sufficient energy drain that they cannot easily survive the subsequent costs of parental care and complete molt (Smith 1995).

THE IMPORTANCE OF FEMALE-BASED QUESTIONS IN BIOLOGY

It was my population of Rufous-collared Sparrows, with its year-round breeding, that gave me my first experience with a social system in which females consistently dominated males. When I moved north from Costa Rica, I began searching through the literature and discovered that breeding female dominance was, in fact, a widespread phenomenon among monogamous birds, although often the reports of it were placed near the end of papers, and began with words such as "Oddly . . ." In combing through the literature, I came across a paper by Margaret Morse Nice (1949) titled "The question of sexual dominance." She had found that in Song Sparrows, females were dominant over males during the breeding season, and had speculated about how widespread this pattern might be. I therefore dedicated my paper on this general pattern in monogamous birds to her (Smith 1980b).

In that paper I brought together reports of breeding female dominance in 37 species from 18 avian families (Table 4). In many of these, males are dominant during the nonbreeding season; here dominance reversal must occur twice a year. I related this reversal

TABLE 4. Monogamous birds with breeding female dominance. Data from Smith (1980a).

Species	Family	Reference	Reversal?
Sula leucogaster	Sulidae	Simmons 1970	No
Accipiter striatus	Accipitridae	Reynolds 1972	No
Falco rusticolus	Falconidae	Cade 1960	No
F. perigrinus	Falconidae	Cade 1960	No
Picoides pubescens	Picidae	Kilham 1974	Yes
Dendrocincla fuliginosa	Dendrocolaptidae	Willis 1972	No
Gymnopithys bicolor	Thamnophilidae	Willis 1967	Yes
Garrulus glandarius	Corvidae	Goodwin 1951	Yes
Parus major	Paridae	Hinde 1952	Yes
Sitta carolinensis	Sittidae	Kilham 1971	Yes
S. canadensis	Sittidae	Kilham 1975	Yes
Sialia sialis	Turdidae	Krieg 1971	Yes
Muscicapa striata	Muscicapidae	Davies 1977	?
Lanius ludovicianus	Laniidae	Miller 1931a	?
Vireo solitarius	Vireonidae	James 1978	?
V. flavifrons	Vireonidae	James 1978	?
Setophaga ruticilla	Parulidae	Ficken 1963	Yes
Icterus galbula	Icteridae	Miller 1931b	Yes
Emberiza calandra	Emberizidae	Andrew 1957	Yes
E. citrinella	Emberizidae	Andrew 1957	Yes
E. schoeniclus	Emberizidae	Andrew 1957	Yes
Melospiza melodia	Emberizidae	Nice 1943	Yes
Zonotrichia capensis	Emberizidae	Smith 1978b	?
Carduelis carduelis	Carduelidae	Hinde 1956	Yes
C. tristis	Carduelidae	Coutlee 1967	Yes
C. lawrencei	Carduelidae	Linsdale 1957	Yes
C. psaltria	Carduelidae	Linsdale 1957	Yes
C. flammea	Carduelidae	Dilger 1960	Yes
Carpodacus purpureus	Carduelidae	Thompson 1960	No
C. cassinii	Carduelidae	Samson 1977	No
C. mexicanus	Carduelidae	Thompson 1960	No
Loxia curvirostris	Carduelidae	Tordoff 1954	Yes
Pyrrhula pyrrhula	Carduelidae	Hinde 1956	Yes
Chloris chloris	Carduelidae	Hinde 1956	Yes
Coccothraustes coccothraustes	Carduelidae	Hinde 1956	Yes
Fringilla montifringilla	Fringillidae	Hinde 1956	Yes
F. coelebs	Fringillidae	Marler 1956	Yes

to the relative costs to the two sexes in different seasons of the year. For males, high rank in the nonbreeding season can be of extreme importance, as it may affect the quality of breeding territory that can be obtained in the spring. Those having the poorest rank may not get a territory at all and, since males in many species outnumber females, only males with the best territories are ensured of acquiring mates. Low winter rank to a female will have little direct effect on her breeding success the following spring, but to a male, it may prevent him from breeding at all. Thus, in the nonbreeding season, the advantages of dominance to a male will be greater than the disadvantages of subordination to the female. However, during the breeding season the reverse is true. The enormous costs of egg production (often entirely overlooked in papers assessing costs of parental care) makes the early breeding season a period of critical importance to females. If dominance permits a female to obtain more food during this period, it could give her a clear advantage over more subordinate females. At the same time, resident males, who have succeeded in obtaining a territory and a mate, actually may benefit from their mate's dominance if it results in higher quality of their offspring. Thus, during the breeding season, the advantages of domi-

nance to a female are greater than the disadvantages of subordination to the male (Smith 1980b).

In my Rufous-collared Sparrow population in Costa Rica, only one class of birds could supplant adult females: the dependent juveniles. This observation got me thinking about the kinds of behavior so often referred to as "begging" in birds. Begging occurs in two common situations: by the female during courtship feeding and by dependent fledglings in family flocks. However, courtship feeding happens at the peak of female dominance, and the literature contains many reports of dependent fledglings, such as my sparrows, being dominant over adults (e.g., Marler 1956; Willis 1967, 1968). The word "begging" contains a lot of unspoken implications that, on careful examination, are not supported by facts. Indeed, the birds doing the so-called "begging" typically are dominant over the birds that respond by giving them food. I therefore proposed that it would be more accurate to term this kind of activity "demand behavior" (Smith 1980c).

The interpretation of the rapid wing movements variously called "fluttering" or "quivering" often seems to be based on unspoken assumptions. Perhaps because it often is given by females in sexual contexts, it has frequently been termed "appeasement displays" (e.g., Hardy 1961, Zahavi 1971), even when applied to females in the early breeding season, the time when their dominance over males typically is most pronounced. I suspect this illustrates circular reasoning: females do this, so it must be appeasement, and since females are doing this appeasement behavior, they must be subordinate. I suspect that most wing fluttering behavior may be a kind of threat display, perhaps being elicited in situations of strong conflict of opposing drives, as shown by Jones (1968) for Great Tits (*Parus major*). Certainly rapid fluttering wing movements in both captive and free-living Loggerhead Shrikes are anything but appeasement; rather, they are highly aggressive in nature (Smith 1973c).

Breeding female dominance, being such a widespread pattern in monogamous birds, also may be a factor in the so-called "reverse" size dimorphism found in raptors. In species such as chickadees or Song Sparrows, interactions involved in dominance reversal will not be particularly dangerous. In contrast, raptors, with their talons and powerful hooked bills, have the ability to inflict real damage. Female raptors' much bigger size may ensure their dominance without the necessity of establishing dominance through agonistic encounters. It is interesting here that the accipiters, which eat primarily birds, show perhaps the most pronounced size dimorphism among avian raptors (Smith 1982).

Not long ago I read one too many papers based on two unstated, unexamined assumptions concerning female behavior (or the lack thereof). Many suggest or state outright that the vast majority of extrapair copulations (EPCs) are the result of the resident male's failure to drive off male intruders. One unstated assumption here is that females never move beyond the boundaries of their home territory. Another is that females will mate unquestioningly and unselectively with any male that approaches her. I found both of these assumptions decidedly hard to believe.

I decided to test these assumptions with Black-capped Chickadees. I used field notes from my two previous color-banding studies to add to my current observations, and accumulated 13 records of EPCs in which all three birds (the female, her mate, and the other male) were color banded and their winter ranks known.

In all 13 of the EPCs, the "other" male had ranked above the female's own mate during the past winter (Table 5). Furthermore, in nine cases, the EPCs occurred in the territory of the other male. Thus, females were being highly selective of their EPC partners, and typically left their own territories in active search of superior chickadees (Smith 1988b). More recently, DNA fingerprinting studies have supported the idea that female chickadees prefer high-ranked males as EPC partners (Otter et al. 1994, 1998, 1999). The pattern of females leaving their own territory to approach better quality partners is now known to be quite common, as shown by the work of Stutchbury and her colleagues on Hooded Warblers (*Wilsonia citrina*; Stutchbury et al. 1994, 1997; Neudorf et al. 1997; Tarof et al. 1998; see also Morton et al. 2000, Kempenaers et al. 1992, and Westneat et al. 1990).

A number of papers (see Smith 1988b) have suggested that male floaters might "sneak

TABLE 5. Extrapair copulations in Black-capped Chickadees. Data from Smith (1988b).

Year	Place[a]	Rank of mate	Rank of other male	Location of EPC
1963	BC	2	1	Other male
1963	BC	2	1	Other male
1963	BC	2	1	Other male
1963	BC	2	1	Own male
1964	BC	2	1	Other male
1964	BC	2	1	Other male
1964	BC	2	1	Own male
1971	E.MA	3	1	Other male
1982	W.MA	2	1	Own male
1982	W.MA	3	2	Other male
1984	W.MA	2	1	Own male
1985	W.MA	3	1	Other male
1986	W.MA	2	1	Other male

[a] BC = British Columbia (Vancouver), E.MA = eastern Massachusetts (Wellesley), W.MA = western Massachusetts (South Hadley).

EPCs" with resident females. This strikes me as extremely unlikely. Breeding females typically are dominant over males (Smith 1980b), and thus in most species could reject any unwanted approaches. Breeding season floaters usually are birds that have lost in competition for breeding territories, so presumably the female's own mate is both higher-ranked and more fit than any floater. Thus, the chances of any resident female permitting EPCs with male floaters seem to be very slim indeed. On the other hand, female floaters just might engage in EPCs with resident males. Gowaty and Karlin (1984) have found multiple maternity in Eastern Bluebirds (*Sialia sialis*); it is conceivable that female floaters might mate with local territorial males, then attempt to "dump" the resulting egg(s) in nests nearby. Careful field work combined with DNA fingerprinting techniques might find this to be a not uncommon pattern.

Margaret Morse Nice's autobiography is titled "Research is a passion with me" (Speirs 1979), and so it is for me. My studies have led me to unexpected turns and twists in roads I had thought to be straight and direct; avian research has been, and continues to be, my great delight. Margaret Morse Nice has set a shining example, and I am honored to be following in her footsteps.

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Short Communications

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First Description of the Nest of the Silvery-fronted Tapaculo (*Scytalopus argentifrons*)

Bruce E. Young[1,3] and Willow Zuchowski[2]

ABSTRACT.—We describe a nest of the Silvery-fronted Tapaculo (*Scytalopus argentifrons*), a member of a large genus in which only one-fourth of the species have described nests. The nest, found in a Costa Rican cloud forest and containing two chicks, was a substantial globular structure constructed mostly of moss, located in a subterranean cavity at the end of a short, narrow tunnel. *Received 27 June 2002, accepted 19 November 2002.*

Despite its widespread distribution in Central and South America and its large number of species, the tapaculo genus *Scytalopus* (Rhinocryptidae) remains poorly known. Individuals of most species skulk in thick vegetation and rarely are seen, although their frequent, distinctive calls readily give away their presence. Many species have similar, drab plumages, and their taxonomic distinctions are not clear (Krabbe and Schulenberg 1997, Coopmans et al. 2001). Ornithologists have described the nests of only eight of the approximately 36 currently recognized species: *S. latrans* (Skutch 1972, as *S. unicolor*), *S. micropterus* (P. Gertler in Hilty and Brown 1986, as *S. femoralis*), *S. indigoticus* (A. Ruschi in Sick 1993), *S. magellanicus* (Johnson 1967), *S. simonsi* (T. Schulenberg in Rosenberg 1986, as *S. magellanicus*), *S. canus* (T. K. Salmon in Sclater and Salvin 1879, as *S. magellanicus*), *S. fuscus* (Johnson 1967, as *S. magellanicus fuscus*), and *S. superciliaris* (Stiles 1979). These nests tend to be globular, constructed of root fibers and mosses, and located in a crevice or in an earthen cavity, often on a steep slope.

The Silvery-fronted Tapaculo, *S. argentifrons*, is the only member of its family to extend substantially into the Central American isthmus, occurring in montane forest from about 1,500 m to timberline in western Panama through northern Costa Rica (Stiles and Skutch 1989, American Ornithologists' Union 1998). Typical for the genus, it occupies dense thickets, often in ravines or steep hillsides. Rarely seen, evidence from vocalizations nevertheless indicates that it is common in old growth and adjacent second growth forest throughout its range. Here we provide the first description of its nest.

WZ discovered the nest 2 m from a well-traveled trail on 7 April 2001 at an elevation of 1,500 m in the Monteverde Cloud Forest Preserve, Monteverde, Puntarenas Province, Costa Rica (10° 18′ N, 84° 48′ W; detailed description in Haber 2000). She heard an abbreviated call of an adult, followed by cries that sounded like nestlings. She then observed an adult Silvery-fronted Tapaculo enter an inconspicuous opening in the steep hillside. The cries increased in intensity until the adult left.

We returned five days later to re-examine the site. Upon arrival, we heard a constant insect-like chirping coming from the vicinity of the nest. This noise gave way to a much louder begging sound when an adult arrived to feed the young. The nest was at the end of a short earthen tunnel that was just large enough to reach in and feel two well-feathered chicks. We then stood back 3 m from the nest and observed adults make feeding visits (indicated by the arthropods visible in their bills) approximately every 15 min.

The nest was empty on our next visit (19 April), so we excavated it (deposited in the Museo Nacional de Costa Rica, MNCR259). The nest was located about one meter from the edge of an approximately 10 × 30 m regenerating treefall gap in an area with many shrubs and small trees, including hibiscus (Malvaceae: *Malvaviscus palmanus*), melas-

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FIG. 1. View of entrance to tunnel leading to the nest cavity of Silvery-fronted Tapaculo (*Scytalopus argentifrons*) in montane cloud forest, Costa Rica, 12 April 2001. Arrow marks thin veil of moss covering entrance. Photograph by W. Haber.

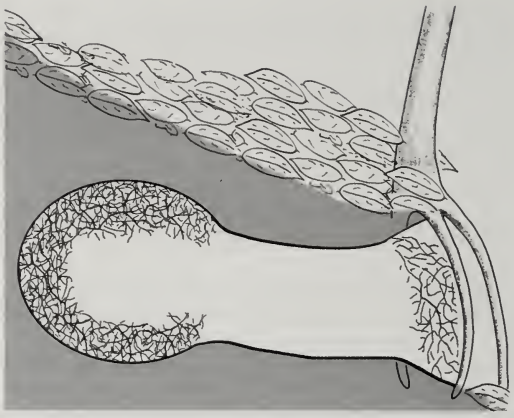

FIG. 2. Schematic cross-sectional view of subterranean nest of the Silvery-fronted Tapaculo (*Scytalopus argentifrons*), Costa Rica. Drawing by Willow Zuchowski.

tome (Melastomataceae: *Ossaea micrantha*), coffee (Rubiaceae: *Psychotria* sp.), aster (Asteraceae: *Koanophyllon pittieri*), acanthus (Acanthaceae: *Razisea spicata*), and nettle (Urticaceae: *Urera elata*). The canopy was a mix of advanced secondary and old growth cloud forest trees where avocado (Lauraceae: *Ocotea tonduzii*) predominated. The nest entrance was framed by the 1-cm diameter stilt roots of an *Ossaea micrantha*, and the entrance itself covered by a veil of fine moss fibers (Figs. 1 and 2). The entrance was about 7 cm wide × 9 cm high and then narrowed to a 12-cm long tunnel. The nest cavity measured 8–10 cm wide × 8 cm tall. The top of the nest cavity was 2–3 cm below the soil surface, which was covered by another 3–5 cm of leaf litter that had collected on the uphill side of the *O. micrantha* trunk.

The nest had a flattened, globular form (Fig. 1). Much of the nest material consisted of fine mosses, including *Frullania* sp., *Plagiochila* sp., and *Phyllogonium viscosum*, most of which had lost their thalluses. Other material included fungal rhizomorphs (*Marasmius* spp.), a few short segments of bird bones, and coleopteran elytra. The upper half of the nest was considerably bulkier than the bottom (upper half, 6.24 g dry mass; lower half, 3.67 g). We observed no nest lining. Attached to the nest material we found pupae of the flea *Dasypsyllus gallinulae perpinnatus* (Ceratophyllidae), a common ectoparasite of nestling birds (flea vouchers deposited in the California Academy of Sciences).

This nest of *Scytalopus argentifrons* thus is typical of the few so far described for the genus; it is subterranean, has an obscured entrance, and is constructed mostly of moss. Previous authors have not reported a difference in the thickness between the top and bottom. We hypothesize that the bulky upper portion of the nest served to soak up water that would otherwise percolate through the soil and into the nest in its typically damp habitat. Supporting this assertion is our observation that when we collected the nest, the upper portion was much damper than the lower portion. Although we found the nest at the end of the dry season in Monteverde, precipitation still is frequent and the leaf litter often is saturated (Clark et al. 2000). Other tropical tapaculos can nest during the rainy season. Skutch (1972) found the *S. latrans* nest in October, during peak rainy season in the eastern Ecuadorian Andes (Ridgely and Greenfield 2001). Similarly, the timing of the *S. micropterus* nest also corresponded with the rainy season of southeastern Colombian Andes (Hilty and Brown 1986). South temperate *Scytalopus* breed during the austral spring when temperatures rise (Johnson 1967).

Scytalopus vary in the extent to which they utilize tunnel entrances. One *S. micropterus*

nest had a 5- to 7-cm entrance runway and an *S. fuscus* nest had a 60-cm entrance corridor running through vegetation, but the described nests of congeners apparently do not have tunnels (Johnson 1967, P. Gertler in Hilty and Brown 1986). The specialized shape of the tunnel and cavity used by *S. argentifrons* suggests that the adults excavate the structure themselves. Of the vertebrates in Monteverde that excavate small holes, such as the Blue-crowned Motmot (*Momotus momota*), Gray-throated Leaftosser (*Sclerurus albigularis*), and Cherrie's pocket gopher (*Orthogeomys cherriei*), none make holes as short or narrow as the hole of the Silvery-fronted Tapaculo we observed (Stiles and Skutch 1989).

Our observations suggest how nest architecture may be an adaptation of the Silvery-fronted Tapaculo for living in a very humid environment. Future observations of nests of this and other *Scytalopus* species could determine the generality of this feature and, together with descriptions of eggs and chicks, enhance the understanding of taxonomic relationships in the group.

ACKNOWLEDGMENTS

We thank the Tropical Science Center for allowing us to perform observations at their Monteverde preserve, and the Costa Rican Servicio de Vida Silvestre for issuing a permit to W. Haber, who collected the nest. We thank W. Haber for confirming our woody plant identifications, M. I. Morales for identifying the mosses, J. Carranza for identifying the fungus, and R. Lewis for identifying the fleas. Finally, we are grateful to K. Zyskowski and F. G. Stiles for suggesting references and commenting on previous drafts of this manuscript.

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First Report of a Double-brooded Swainson's Warbler

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ABSTRACT.—Here I report the first case of double brooding in a Swainson's Warbler (*Limnothlypis swainsonii*). On 7 June 2002, I observed a color-banded female feeding an 8-day-old fledgling 20 m from her first nest. On 12 July 2002, I saw the same bird feeding a banded 12-day-old fledgling 8 m from her second nest. Double brooding is one strategy by which a genotype may increase genetic representation in future generations. *Received 30 September 2002, accepted 1 March 2003.*

While most Temperate Zone wood warblers are primarily single brooded (Morse 1989), studies of marked individuals have shown double brooding was an uncommon but regular occurrence in several species. Two studies found up to 77% of female Prairie Warblers (*Dendroica discolors*) and Prothonotary Warblers (*Protonotaria citrea*) that successfully reared a first brood attempted a second brood (Nolan 1978, Petit 1989). Holmes et al. (1992) found double brooding was the most important cause of high annual production in Black-throated Blue Warblers (*Dendroica caerulescens*). Also, a study of Hooded Warblers (*Wilsonia citrina*) showed that double-brooded females produced a mean of 60% more fledglings than single-brooded females (Ogden and Stutchbury 1996). Here I report the first observation of double brooding in a Swainson's Warbler.

I found both nests in the Horse Pasture region of the Franklin L. Gravely Wildlife Management Area, Pickens County, South Carolina (36° 02′ N, 82° 50′ W). The topography of the management area was mountainous. The nest sites were dominated by second growth (15- to 20-m tall) yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and Canada hemlock (*Tsuga canadensis*). The understory was composed of giant rhododendron (*Rhododendron maxium*), dog hobble (*Leucothoe fontanesiana*) and young Canada hemlock. Both nests had been built in Canada hemlocks growing in an abandoned railroad bed and were 10–20 m from a 3-m wide mountain stream.

On 2 May, I found the first nest in the approximate center of the 250-m diameter breeding territory of a banded male. The nest was 2.1 m above the ground on an eastward projecting limb of a 4-cm (dbh) Canada hemlock. On 8 and 10 May the nest was still empty. On 13 May the nest contained three white eggs. If nest construction took 2–3 days (Meanley 1969) and the first egg was deposited 2–4 days after that (Meanley 1971), then nest construction probably began on about 2 May and the first egg deposited on 11 May. On 15 May the nest contained four eggs. If the clutch increased by one egg each day, the fourth egg would have been deposited on 14 May; incubation likely began the same day (Meanley 1971). On 24 May I flushed the incubating female from the nest into a mist net and applied colored plastic leg bands. At 09:36 EST on 29 May, no eggs were pipped. At 10:35 on 31 May four nestlings were in the nest.

On 7 June I observed both banded adults chirping loudly and rapidly about 20 m east of the first nest. I saw the banded female carry food items to a fledgling Swainson's Warbler. Swainson's Warblers typically fledge 10 days (Sims and DeGarmo 1948, Meanley 1969) to 12 days (Sprunt et al. 1957) after hatching. Later that day, I found the first nest very wet and on the ground. It appeared intact and there was no obvious damage. About 1 m from the nest I found the partially eaten remains of one fledgling.

On 12 June I discovered the second nest 109 m west of the first nest. The second nest was 1.9 m above the ground in a 6-m tall, 6.3-cm dbh Canada hemlock. This nest was 15 m east of the western edge of the breeding territory of the same banded male. At 10:00 on 14 June, one white egg was present. Based on the same criteria presented above, I estimated that the construction of the second nest may have begun as early as 8 June. I observed four

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white eggs on 17 June. The second nest contained three nestlings and one complete egg on 1 July. On 8 July I banded the three nestlings and salvaged the infertile egg. Also on this date, I confirmed the identification of the female and male as they brought food items to the nest. At 07:25 on 12 July the second nest was empty. I observed the banded female carrying food items about 8 m southeast of the nest, where she fed a banded 12-day-old fledgling that was perched 1 m above the ground on a rhododendron limb.

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Use of Northern Cardinal Nest by Fledgling Carolina Wrens

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ABSTRACT.—We report on the use of a Northern Cardinal (*Cardinalis cardinalis*) nest by fledgling Carolina Wrens (*Thryothorus ludovicianus*) during a period of inclement weather. We found four fledgling wrens in a newly lined cardinal nest on the morning of 22 May 2002 during a heavy frost. The use of the cardinal nest by the wrens may have been precipitated by the unexpected frost. This represents a unique method of protection from inclement weather taken by young birds. *Received 6 August 2002, accepted 23 February 2003.*

Recently fledged young of some species return to their natal nests to roost (Preble 1961, Verner 1965, Johnson and Cowan 1974, Koenig et al. 1995), but interspecific nest use for roosting or shelter is less well documented (Kennedy and White 1997). Here we describe the use of a Northern Cardinal (*Cardinalis cardinalis*) nest by four fledgling Carolina Wrens (*Thryothorus ludovicianus*).

We observed the following during a study focusing on Northern Cardinals at Aullwood Audubon Center and Farm (39° 52′ N, 84° 16′ W), 15 km northwest of Dayton, Ohio. On 20 May 2002, JMJ found a new unlined nest (presumed to be a cardinal nest) that was approximately 1 m above the ground in a bush honeysuckle (*Lonicera mackeii*). Following the initial nest discovery, we observed a banded female cardinal (USFWS aluminum band plus three plastic color bands) adding material to the nest. On 22 May 2002, at approximately 08:00 EST, we checked this nest to determine

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if the female cardinal had finished building the nest and begun to lay eggs. We observed four birds in the nest that, upon flushing from the nest, were identified as Carolina Wrens. Based on appearance, size, and the arrival of two scolding, adult Carolina Wrens from the nearby bushes, we assumed that the four smaller birds were fledglings. The fledglings and their parents stayed in the vicinity of the cardinal nest for the remainder of the morning and then moved away from the nest.

The wrens apparently had fledged from a nest box placed outside a nearby house approximately 50–60 m from the cardinal nest in which they were found (J. Wilson pers. comm.). We believe the wrens fledged from their nest on 21 May 2002 (J. Wilson pers. comm.). The use of the cardinal nest may have been precipitated by an unexpected freeze that occurred during the early morning of 22 May 2002. The low temperature of the morning was 0° C (J. Simpson pers. comm.), and we observed frost in shaded areas until about 09:00 EST. The same female cardinal that built the nest (based on color band combination) began laying eggs there on 23 May 2002 and successfully fledged a brood of young. Apparently, the female cardinal that built the nest was undisturbed by, or unaware of, the presence of the wrens in the nest.

In many species, including Carolina Wrens (Haggerty and Morton 1995), fledglings are known to roost together for warmth and protection. Breeding and nonbreeding adult Carolina Wrens have been observed sheltering in nest boxes, as well as in a variety of other places, including old bird's nests (possibly Northern Cardinal nests; Haggerty and Morton 1995, T. M. Haggerty pers. comm.). Given that adult wrens use many different types of shelter for roosting, our observation indicates that this behavior may begin early in life.

It is possible that wrens, in general, are prone to use nests as a form of shelter. House Wren (*Troglodytes aedon*) and Marsh Wren (*Cistothorus palustris*) fledglings have been observed roosting in their natal nests (Preble 1961, Verner 1965). Adult Carolina Wrens and fledgling Bewick's Wrens (*Thyomanes bewickii*) have been observed roosting in the nests of other species (Haggerty and Morton 1995, Kennedy and White 1997). Given that several members of the family Troglodytidae are well known for building nests opportunistically in unusual sites, wrens may be more flexible in adopting novel roosting places as well. Interspecific nest use may represent a flexible, yet adaptive, protection strategy by fledglings faced with unexpected and potentially dangerous inclement weather.

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Golden-fronted Woodpecker Provisions Nestlings with Small Mammal Prey

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ABSTRACT.—On 11 April 2002, in San Pedro, Belize, we observed a male Golden-fronted Woodpecker (*Melanerpes aurifrons dubius*) cache a mouse carcass and subsequently provision nestlings with tissue taken from it. During 12 min of observation, the male made seven trips with pieces of the carcass, taking pieces of muscle to the nestlings and consuming skin and connective tissue himself. This is the first published record of the consumption of mammalian prey by this species. *Received 14 June 2002, accepted 7 December 2002.*

The natural history of the Golden-fronted Woodpecker (*Melanerpes aurifrons*) is poorly known, particularly for many of the subtropical and tropical races of this species. Data on the range of food items delivered to nestlings are especially limited. Here, we report an observation of a male Golden-fronted Woodpecker (*M. a. dubius*) in Belize provisioning nestlings with tissue pecked from the carcass of a small mammal.

We first observed the male at 07:30 CST on 11 April 2002 on the grounds of the Caribbean Villas Hotel in San Pedro, Ambergris Caye (17° 54′ N, 87° 58′ E), Belize. As we watched from a distance of approximately 10 m, the male flew with a carcass in its bill to an abandoned wooden utility pole. The male perched approximately 10 m above the ground on the bottom edge of a shallow, irregular crevice in the pole and proceeded to wedge the carcass into the depression. At this time, we determined that the carcass was a small mammal, probably a mouse. The pelage was almost entirely dark gray, and we saw a thin, furry tail approximately equal in length to that of the body (about 7–10 cm total length). The carcass was mostly intact, but the skin appeared to have been torn in a few places.

Using the jagged edges of the crevice to anchor the carcass, the male pecked it repeatedly with slow and deliberate strokes, stopping briefly to pull off and consume bits of skin and hair. The male then removed three or four pieces of what appeared to be muscle tissue from the carcass and flew approximately 50 m to a nest cavity in a coconut palm (*Cocos nucifera*) snag. When the male arrived at the nest, we could hear nestlings begging inside. After a few seconds, the male almost completely entered the nest, withdrew with its bill empty, and returned immediately to the carcass cached in the utility pole. As before, the male pecked at the carcass repeatedly, tearing from it bits of skin and translucent connective tissue that he consumed. On one occasion, the male picked up the entire carcass and wedged it back into the crevice. The male then removed three or four more pieces of dense pink tissue and flew to the nest cavity. After feeding the nestlings, the male returned to the mouse carcass to collect more food. His efforts were interrupted when he called twice to his mate as she returned to the nest cavity with a bill full of food. The female responded while approaching the nest but did not call again as she flew away after feeding the nestlings. The male returned his attention to the carcass and pecked at it as before, this time ripping the tail from the carcass and consuming it before he flew back to the nest with three more pieces of muscle tissue.

The male continued to provision the nestlings in this fashion until 07:42 when he flew from the nest cavity without returning to the mouse carcass. Between 07:31 and 07:42 the male made a total of seven visits to the nest with tissue from the carcass. During his final visit to the carcass, he removed a large, yellow mass of viscera and dropped it to the ground. He then removed an approximately 5-mm piece of muscle tissue and delivered it to the nest cavity. We searched for the tissue that the male dropped but could not find it in the surrounding low vegetation.

Although data on the foraging ecology of this species are limited, Golden-fronted

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Woodpeckers are known to be omnivorous and opportunistic (Husak and Maxwell 1998), as are their closest relatives, the Red-bellied (*Melanerpes carolinus*; Shackelford et al. 2000) and Gila (*M. uropygialis*; Edwards and Schnell 2000) woodpeckers. Animal matter consumed by Golden-fronted Woodpeckers includes a variety of insects and spiders (Kujawa 1984, Husak and Maxwell 1998), and possibly bird eggs (Husak 1995). Husak and Maxwell (1998) reported that one individual was observed to have killed and possibly eaten a *Sceloporus* lizard, and in another study an individual was observed consuming marrow from a bone (Kujawa 1984). Almost no data are available, however, on the food items that adult Golden-fronted Woodpeckers deliver to their nestlings. In westcentral Texas, such items reportedly include insects, spiders, and berries (Husak and Maxwell 1998).

This apparently is the first published record of an adult Golden-fronted Woodpecker consuming and provisioning nestlings with mammalian prey. The consumption of mammalian prey (mice) has been observed in only one other species in the genus *Melanerpes*, the Red-headed Woodpecker (*M. erythrocephalus*), though very infrequently (Smith et al. 2000). Adult Red-headed Woodpeckers occasionally have been observed to consume other vertebrates as well, including dead fish (Southern 1966), small lizards (Belson and Small 1998), and nestling Cliff Swallows (*Petrochelidon pyrrhonota*; citations in Smith et al. 2000). The more closely related Gila Woodpecker also has been observed to consume small lizards (Phillips et al. 1964) and meat scraps (beef bones and bacon rind; Bailey 1923).

We do not know whether the male Golden-fronted Woodpecker described in this report killed the mouse that he cached and fed to his nestlings, but it is possible given that other species in this genus prey on live vertebrates. Alternatively, Golden-fronted Woodpeckers are opportunistic in their foraging habits and the male we observed might have discovered the mouse after it had died. Our observation underscores the omnivorous foraging habit of this species and provides unique information on the range of food items delivered to nestlings.

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Water Loss from Eggs of the Great Frigatebird

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ABSTRACT.—The natural incubation period of Great Frigatebird (*Fregata minor*) eggs reported in the literature (55 days) was 74% longer than the value predicted from initial egg mass (89.1 g). The long incubation period was associated with a low daily water loss (213.5 mg/day) from the eggs and few pores in the eggshell (4,643 pores/egg). The initial event in the pipping process, which represented 7.2% of the duration of the incubation period but accounted for 24.9% of the total water loss from the egg, was a star-shaped fracture of the shell which increased water loss from the egg and persisted for several days before hatching was complete. These characteristics of the eggs of the Great Frigatebird are contrasted with those from the Red-footed Booby (*Sula sula*), the only other altricial, pelecaniform seabird with a long incubation period, for which data are available. *Received 7 May 2002, accepted 19 November 2002.*

In many semiprecocial tropical seabirds, daily water loss from the eggs over the extended incubation period is curtailed by a relatively small number of pores in the eggshell through which water vapor diffuses out of the egg (Whittow 1980, 1984). However, in the Red-footed Booby (*Sula sula*), an altricial, pelecaniform seabird with prolonged incubation, low water loss from the eggs is associated with a thick, chalky eggshell rather than with few pores in the shell (Whittow et al. 1989). The purpose of this study was to obtain data for the eggs of another altricial pelecaniform seabird with prolonged incubation, the Great Frigatebird (*Fregata minor*), and to compare them with those of the Red-footed Booby.

METHODS

We made observations at Great Frigatebird colonies in the Northwestern Hawaiian Islands, including Green Island, Kure Atoll (28° 24′ N, 178° 18′ W); Eastern Island, Midway Atoll (26° 12′ N, 177° 20′ W); and East Island, French Frigate Shoals (23° 52′ N, 166° 17′ W).

We determined water loss from 10 unpipped eggs by weighing the eggs at intervals of 47.2 h to 7 days (Drent 1973, Rahn and Ar 1974) on an Ohaus field balance (Model 1010–10) at the nest site. We measured the temperature of six incubated eggs by inserting a fast response needle thermistor probe into each egg. This procedure required approximately 15 s. All egg temperatures were taken from the center of the egg and were measured by connecting the thermistor lead to a YSI Telethermometer. We determined initial mass (corresponding to the mass of the freshly laid egg) by weighing 14 collected eggs after their air cells had been filled with distilled water (Grant et al. 1982). We determined egg volume by weighing the eggs in air and in water (Rahn et al. 1976), and we used a dial caliper to measure linear dimensions.

We measured water vapor conductance of the shell and shell membranes by weighing 14 freshly collected eggs, which were kept in a desiccator at 25° C for 1 week (Ar et al. 1974). Eggshell mass and thickness were measured on shells that had been dried in a desiccator for at least 1 week. We used a micrometer caliper, fitted with a ball attachment on the spindle to accommodate the curvature of the eggshell, to measure eggshell thickness at 7 locations on each of six eggs. We counted the number of pores in the shells (pore density) by the method described by Tyler (1953) and Roudybush et al. (1980). We calculated the total functional pore area and the total number of pores in the shell as described by Tullet and Board (1977) and Ar and Rahn (1985).

We collected six eggs on Tern Island to observe the pipping phase of incubation. These eggs were incubated in a laboratory incubator at the Univ. of Hawaii at a temperature of 37° C and a relative humidity of 60%, turned through 180° twice daily, and examined for signs of pipping. External pipping was recognized by a protruding fracture of the shell, while internal pipping was identified by "cheeping" sounds made by the embryo, and also by candling the egg (Pettit and Whittow

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TABLE 1. Characteristics of Great Frigatebird eggs and eggshells.

Variable	Observed		Predicted
	Mean ± SD	Number of eggs	
Eggs			
Initial mass (g)	89.1 ± 6.8	14	—
Volume (cm^3)	83.3 ± 6.4	14	—
Length (cm)	7.0 ± 0.3	26	—
Width (cm)	4.8 ± 0.9	26	—
Water loss (mg/day)	213.5 ± 33.1	10	368.1[a]
Temperature (°C)	36.8 ± 0.8	6	—
External Pipping			
Mean duration (h)	33.7 ± 17.2	6	—
Mean water loss (mg/h)	17.9 ± 4.1	7	—
Internal Pipping			
Mean duration (h)	48.3 ± 10.9	6	—
Mean water loss	21.5 ± 3.4	8	—
Pip hole phase			
Mean duration (h)	40.7 ± 17.1	6	—
Mean water loss (mg/h)	60.8 ± 25.2	13	—
Eggshells			
Water-vapor conductance (mg/day torr)	7.5 ± 1.2	14	14.9[a]
Shell thickness (mm)	0.37 ± 0.02	7	0.039[a]
Shell mass (g)	6.60 ± 0.56	8	
Pore density (pores/cm^2)	56.9 ± 9.0	7	99.1[b]
Total functional pore area (mm^2)	1.26	—	2.52[a]
Number of pores/egg	4,643	—	9,518[a]

[a] Equations from Ar and Rahn (1985).
[b] Equation from Tullet and Board (1977).

1983). We weighed these eggs to the nearest 0.1 mg at intervals of 7.2–24 h, and we weighed hatchlings to the nearest 1 mg.

RESULTS

Observed and predicted values for egg and eggshell variables are presented in Table 1. Information on the events immediately before hatching in naturally incubated eggs was obtained from only one egg. This egg, which was not pipped when first examined, had a large pip hole 64.0 h later. When next observed, 23.3 h later, the egg had hatched. Thus, the egg was pipped for less than 87.2 h.

For the six artificially incubated eggs, the initial event in the pipping process was a star-shaped fracture of the shell (external pipping) which occurred a mean of 94.6 h ± 13.3 SD prior to hatching. For three of these eggs, external pipping was followed a mean of 23.5 h ± 10.2 SD later by internal pipping, and a distinct pip hole was not formed until a mean of 32.4 h ± 6.9 SD before hatching. In two eggs, external and internal pipping were detected at the same time and these phases were followed by the formation of a pip hole. In the sixth egg, external pipping was followed by the formation of a pip hole in the shell; internal pipping (puncture of the shell membranes) was not detected until 11.3 h later. Thus, external pipping was always the initial event in the pipping process, although, in two instances, it was accompanied by internal pipping. All eggs had pip holes immediately prior to hatching.

Analysis of variance did not detect significant differences in duration among the three phases of pipping (Table 1; $F_{2,15} = 1.42$, $P = 0.22$). Water loss from the eggs increased significantly after pipping (ANOVA, $F_{3,29} = 19.98$, $P < 0.0001$). Analysis of three eggs revealed a statistically significant increase in water loss when unpipped eggs became externally pipped (paired test, $t = 4.35$, df = 2, P

= 0.049). All six artificially incubated eggs hatched successfully; mean hatchling mass was 58.38 g ± 3.86 SD. The hatchlings were completely devoid of plumage but their eyes were open.

DISCUSSION

Many allometric relationships for avian eggs are based on initial egg mass (Carey 1983). One such relationship, based on data for 156 species of birds (Ar and Rahn 1985), predicts that the incubation period for Great Frigatebird eggs, weighing about 89 g, should be about 32 days. Thus, the reported natural incubation period of Great Frigatebirds (55 days; Nelson 1976) is >70% higher than that for birds in general. Prolonged incubation is common in tropical seabirds and it is associated with offshore feeding (Sotherland and Rahn 1987, Whittow 2002). The incubation period of the Great Frigatebird is one of the longest for any tropical, altricial seabird.

In the Great Frigatebird, prolonged incubation is associated with relatively few eggshell pores, rather than a thick eggshell as in the Red-footed Booby (Whittow et al. 1989). The two species differ also in their sequence of events during pipping; the initial event in Great Frigatebird eggs involved fracture of the shell, and calculations similar to those reported for the Red-footed Booby (Whittow and Whittow 1988) revealed that the pipping period represented 7.2% of the total incubation period, but it was responsible for 24.9% of the total water loss from the egg during incubation.

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Prothonotary Warbler Eats Lizard

William E. Davis, Jr.[1,3] and Oliver Komar[2]

ABSTRACT.—We observed a male Prothonotary Warbler (*Protonotaria citrea*) eating a 3-cm lizard in Louisiana. There are few reports in the literature of wood warblers taking vertebrate prey, and we found no other record for a Prothonotary Warbler doing so. *Received 21 October 2002, accepted 15 February 2003.*

Among 50 species of wood warblers (Parulidae), only three have been documented as preying on vertebrates: Northern Waterthrush (*Seiurus noveboracensis*) taking a *Desmognathus* salamander and small fish (Eaton 1995), Louisiana Waterthrush (*S. motacilla*) taking small fish and small frogs (Robinson 1995), and Swainson's Warbler (*Limnothlypis swainsonii*) taking small lizards (Brown and Dickson 1994). To our knowledge, there have been no previously published reports of vertebrate prey for the Prothonotary Warbler (*Protonotaria citrea*; see Petit 1999). A recent study of the foraging habitats of Prothonotary Warblers on their wintering grounds in Costa Rica did not detect vertebrate prey (Warkentin and Morton 2000). Here we describe our observation of a Prothonotary Warbler taking vertebrate prey.

On 28 September 2002, we were watching birds in a stand of ornamental live oaks (*Quercus virginiana*) in the patio area outside of the Inter-Continental Hotel and Pan American Life Building in downtown New Orleans, Louisiana. Our attention was directed by another birdwatcher to a Prothonotary Warbler that was attempting to eat a 3-cm lizard. As we began our observation at 09:39 CST, the warbler, identified as male by plumage, was grasping the lizard across the body, and repeatedly clamping down on the prey with his beak. The bird was perched on a nearly horizontal 15-cm diameter branch, 6–7 m above the ground. During the next 4 min, the bird repeatedly mandibulated the lizard, and wiped and pounded it against the branch. On three occasions the warbler attempted to swallow the lizard, positioning it head first and longitudinally in its beak, getting the lizard half swallowed before ejecting it for further bashing. On the fourth attempt, the lizard was ingested in increments until it finally disappeared from view into the warbler's alimentary tract.

Our observations occurred two days after Tropical Storm Isidore had passed over New Orleans, with high winds and 30–50 cm of rain during a 2-day period. A male Prothonotary Warbler had been present in the live oak stand since the storm, and we speculate that the warbler we observed was the same bird, may have been deprived of food as the storm passed, and was accumulating fat reserves for its trans-Gulf migration. The small size of the lizard suggests that it was a juvenile. Louisiana and Northern waterthrushes, Swainson's Warblers, and Prothonotary Warblers all have relatively large beaks for wood warblers, perhaps enabling these warblers to take the occasional vertebrate prey.

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Predation of an Infant Collared Peccary by a Harpy Eagle in Eastern Amazonia

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ABSTRACT.—An adult Harpy Eagle (*Harpia harpyja*) attacked and killed an infant collared peccary (*Pecari tajacu*) at a site in eastern Amazonia. The eagle appeared to have been prevented from removing its prey immediately by surviving members of the peccary herd. Circumstantial evidence suggests that a set of specific factors, including the abundance of peccaries at the site and forest structure, may have facilitated the attack. *Received 21 March 2002, accepted 30 August 2002.*

The world's largest raptor, the Harpy Eagle (*Harpia harpyja*) is known to prey on a variety of small- to medium-sized Neotropical rainforest mammals. Prey items typically are arboreal, primarily primates (Platyrrhini) and sloths (*Bradypus* and *Choloepus*; Rettig 1978, Izor 1985, Peres 1990, Sherman 1991, Galetti and Carvalho 2000), but terrestrial prey, agoutis and fawns, also have been recorded (Rettig 1978). Here we report on the attack of a Harpy Eagle on an infant collared peccary (*Pecari tajacu*), a previously unrecorded prey species.

The study site was a 2,000-ha reserve of primary Amazonian *terra firme* rainforest known as Esplanada, located at 04° 58′ S, 48° 08′ W in the western extreme of the Brazilian state of Maranhão. The reserve is located on a high plateau bordered to the south by plantations of *Eucalyptus*, and to the north by cattle pasture. The Esplanada reserve is surrounded by a number of smaller, isolated fragments of the original forest cover (see Port-Carvalho 2002).

A survey of the reserve's mammal populations conducted during 2001 (Port-Carvalho and Ferrari 2002) indicated that peccaries (*P. tajacu* and *Tayassu pecari*) were relatively abundant in the Esplanada reserve compared to both neighboring fragments and other rainforest sites in eastern Amazonia (Lopes and Ferrari 2000). During standard line transect surveys in the Esplanada reserve, peccaries were observed at a mean rate of 1.1 times per 10 km surveyed, in contrast with sighting rates of no more than 0.23 at other sites.

At approximately 11:15 Brazilian standard time on 15 November 2001, an adult collared peccary was flushed during survey work on a transect at the study site. Vocalizing loudly, the peccary moved rapidly away from the transect, and was accompanied by at least three other peccaries of adult or nearly adult size, based on vocalizations and their movements in the undergrowth. As the observers moved forward, they flushed an adult Harpy Eagle, perched close to the location from which the peccary had started. The perch was the bottom of the loop of a liana 3 cm in diameter and 4 m above the ground.

When the observers reached this location, they encountered the body of an infant peccary lying on the ground. The body was located within 3 m from the initial position of the adult peccary and 5 m from the perch of the Harpy Eagle. The infant appeared to be 4–6 weeks of age (Sowls 1984), and weighed approximately 1.5–2.0 kg. It was freshly killed, although the body was already cold to the touch, suggesting that at least 30 min had passed since death. The only outward sign of injury was a 1-cm long incision in the middle of the left thorax, typical of an attack by a Harpy Eagle, in which the prey's heart is punctured by the eagle's talons (SFF pers. obs.).

Immediately following the attack, the Harpy Eagle may have been impeded from removing its prey by surviving members of the family group. Collared peccaries live in highly cohesive herds, generally of 6–9 individuals (Sowls 1984, Eisenberg and Redford 1999), and it seems unlikely that the infant would have strayed very far from litter mates or other members of the group. It is unclear whether the individual closest to the carcass was the infant's mother, but the fact that the herd had

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remained nearby strongly suggests that there was a collective reluctance to abandon the infant, despite the fact that it had been dead for some time.

This apparently is the first published report of a successful attack on a peccary by a Harpy Eagle. Adult collared peccaries, the smaller of the two Amazonian species, can weigh up to 30 kg (Sowls 1984), so body size clearly is a limiting factor for Harpy Eagles, which weigh up to 9 kg (Sick 1997). The largest prey item recorded by Rettig (1978) was a 9-kg two-toed sloth (*Choloepus didactylus*). Neonatal collared peccaries weigh <1 kg (Eisenberg and Redford 1999), but reach half the adult weight by about four months of age (Sowls 1984). The availability to Harpy Eagles of prey-sized peccaries thus would appear to depend upon breeding patterns in the local peccary population.

Three other factors also may limit the potential of the collared peccary as a prey species for Harpy Eagles. The first is the ability of such a large raptor to fly within the confines of the forest (Eason 1989) to attack animals on the ground successfully (Fowler and Cope 1964). In the present case, the lower strata of the forest at the study site were relatively open in comparison with most other sites in the region (MP-C pers. obs.). The second factor is that peccaries normally are relatively rare, especially in comparison with primates or sloths. In this case, the apparent abundance of peccaries at the study site may have been important. A third possible factor is the highly cohesive social behavior of collared peccaries and the defensive behavior of mothers with infants (Sowls 1984). The circumstances of this attack, and the lack of previous records, suggest that several factors make the collared peccary an unlikely prey species for Harpy Eagles, and that attacks on forest-dwelling peccaries must be very rare.

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An Updated Account of Wading Bird Foraging Behavior

Jay F. Kelly,[1,2,4] Dale E. Gawlik,[1] and David K. Kieckbusch[1,3]

ABSTRACT.—This paper presents an updated account of 34 wading bird foraging behaviors presented by Kushlan (1978a) with findings from later studies for nine wading bird species, including: Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Little Blue Heron (*Egretta caerulea*), Tricolored Heron (*Egretta tricolor*), Great Blue Heron (*Ardea herodias*), Green Heron (*Butorides virescens*), Glossy Ibis (*Plegadis falcinellus*), White Ibis (*Eudocimus albus*), and Wood Stork (*Mycteria americana*). We also include occurrences of the behavior Prey Dropping, which was not described as a foraging behavior in Kushlan (1978a). *Received 23 May 2002, accepted 14 December 2002.*

Kushlan (1976) presented a thorough summary of previously documented foraging behaviors for North American herons (e.g., Meyerriecks 1960, 1962) to provide a source for "standardized terminology, clear understanding of the descriptive aspects of each behavior, and knowledge of the occurrences of various behaviors in different species." The synopsis was expanded to include additional heron species, as well as tactile-feeding behaviors represented by stork relatives and ibises in Kushlan (1978a). Here, these accounts of wading bird foraging behavior are updated with results from later studies for the following species: Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Little Blue Heron (*E. caerulea*), Tricolored Heron (*E. tricolor*), Great Blue Heron (*Ardea herodias*), Green Heron (*Butorides virescens*), Glossy Ibis (*Plegadis falcinellus*), White Ibis (*Eudocimus albus*), and Wood Stork (*Mycteria americana*).

To obtain a list of wading bird behaviors and their definitions, we conducted a literature search for studies on the aforementioned species, published since Kushlan (1976), adding any behaviors not recorded in Kushlan (1976) or Kushlan (1978a) to a revised list (Table 1). Of the 38 behaviors that were listed by Kushlan (1978a), 34 were relevant to the nine species considered here. Definitions for foraging behaviors follow those in Kushlan (1978a). More detailed descriptions for herons can be found in Hancock and Kushlan (1984) and Hancock et al. (1992). The criteria in Rodgers (1983) was used to distinguish among Walking Slowly (≤1 step/s), Walking Quickly (>1≤2 steps/s), and Running (>2 steps/s).

The literature search revealed nine studies on wading bird foraging behavior (Willard 1977, Kushlan 1978b, Bildstein 1983, Hom 1983, Rodgers 1983, Hancock and Kushlan 1984, Kushlan et al. 1985, Gonzalez 1997, Toland 1999) that reported behaviors not recorded for these species in Kushlan (1978a). The behavior described by Toland (1999) as Mid-air Capture was listed in Kushlan (1976) as Standing Flycatching, and is included in Table 1 under that name.

We also observed and included in the revised list the behavior Prey Dropping, in which the focal bird drops the prey it captures rather than consuming it. This behavior was not described in Kushlan (1978a), but was mentioned in Rechnitzer (1956), Kahl (1964), and Kushlan (1979), and appears to occur in relation to transient, superabundant sources of prey, either with regard to the satiation of the focal birds (DEG unpubl. data), or attempts to capture large numbers of fleeing prey (Kahl 1964). Whereas the other studies described the birds merely dropping their prey, our focal birds would continually strike and drop the same injured or dead fish, often until it was stolen by another bird.

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TABLE 1. Foraging behaviors of nine species of wading birds and first report of occurrence[1] following Kushlan (1976).

Behavior	Great egret	Snowy egret	Great blue heron	Tri-colored heron	Green heron	Little blue heron	Glossy ibis	White ibis	Wood stork
Stand And Wait	K	K	K	K	K	K	K1	K1	K1
Walk Slowly	K	K	K	K	K	K	B	B	K1
Walk Quickly	H	K	H	K1	—	K	Ga	Ga	Ga
Running	W	K	K1	K	—	K	Ga	Ga	G
Hopping	K	K	K1	K	—	K	—	—	G
Jumping	—	Ga	K1	Ga	K	Ga	—	—	—
Leapfrog Feeding	K	W	—	K	—	K	—	—	—
Bill Vibrating	W	K	—	—	—	—	—	—	G
Baiting	—	—	—	—	K	—	—	—	—
Tongue Flicking	—	K	—	—	—	—	—	—	—
Standing Flycatching	—	T	K	T	K	—	—	—	—
Gleaning	K	H	K	—	—	K4	—	—	G
Wing Flicking	K	K	K	K	—	K	—	—	K1
Openwing Feeding	—	K	—	K	—	K	—	—	K1
Underwing Feeding	—	K	—	K	—	—	—	—	—
Foot Stirring	W	K	—	K	K	W	—	—	K1
Foot Raking	—	K	—	K	K	K	Ga	Ga	Ga
Foot Probing	Ga	K	—	—	—	—	—	—	—
Foot Paddling	Ha	K	—	—	—	—	—	—	—
Foot Dragging	Ga	K	—	K	—	K	—	—	—
Hovering	K	K	K	K	—	K	—	—	—
Hovering Stirring	—	K	—	K	—	—	—	—	—
Dipping	K	K	—	K	—	K	—	—	—
Plunging	K	Ga	K	Ga	Ha	Ga	—	—	—
Diving	H	H	—	Ga	K	—	—	—	—
Feet First Diving	Ga	Ga	K	Ga	—	K	—	—	—
Swimming Feeding	K	—	K	K	K	—	—	—	—
Head Swaying	W	W	—	—	K1	W	—	—	—
Neck Swaying	W	—	—	—	K1	—	—	—	—
Head Swinging	K1	—	—	—	—	—	K1	K1	K1
Groping	—	—	—	K1	—	—	K1	K1	K1
Probing	H	H	H	—	—	K4	K1	K1	G
Pecking	W	W	Ha	W	—	K1	K1	K1	—
Steal	W	W	W	Ga	K2	K2	—	K2	K2
Prey Dropping	Ga	Ga	—	Ga	—	Ga	—	K3	R1

[1] Key to symbols: Bildstein 1983 (B), Gawlik unpubl. data (Ga), Gonzalez 1997 (G), Hancock and Kushlan 1984 (Ha), Hom 1983 (H), Kushlan 1976 (K), Kushlan 1978a (K1), Kushlan 1978b (K2), Kushlan 1979 (K3), Kushlan et al. 1985 (K4), Rechnitzer 1956 (R1), Toland 1999 (T), Willard 1977 (W).

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Ornithological Literature

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STONECHATS: A GUIDE TO THE GENUS *SAXICOLA*. By Ewan Urquhart. Illustrations by Adam Bowley. Yale Univ. Press, New Haven and London, and Christopher Helm, A&C Black Publishers, Ltd., London. 2002: 320 pp., 14 color plates, 17 range maps, 16 plates of multiple color photographs. $60.00 (cloth).—The Old World has a great variety of small, often brightly colored and generally very attractive turdid genera, the wheatears, nightingales, Old World robins and redstarts, rubythroats and bluethroats, to name a few, which are represented in North America only marginally (by just two species), to our misfortune. The present work deals with only one of those genera, the genus *Saxicola*, comprising fourteen species of mostly Eurasian distribution.

The book starts off with some housekeeping items on sequence and taxonomy, nomenclature, and a section usefully titled "How to use this book." There then follows a guest essay from some German authors on the relationships of stonechats and other turdids, which presents molecular phylogeny diagrams, the overall gist of which will be comprehensible to the nonspecialist reader, and a large amount of molecular genetic data which will not.

The text continues with individual species accounts. These are superbly detailed and comprehensive. For example, there are 30 pages devoted to the first species, the Whinchat (*Saxicola rubetra*). Each account starts with a section on subspecific taxonomy, followed by an essay on identification, with notes on similar species and how to distinguish the Whinchat from them. Next comes a major section titled "Description," which in exhaustive feather-by-feather detail describes the different plumages of the sexes and ages, ending with measurements. In the case of polytypic species, each race is given separate treatment. Then comes distribution and status, accompanied by large, clear and detailed maps which are easy to read, despite the use of halftones (in pleasing contrast to, for example, the range maps in the *Handbook of birds of the world*). For polytypic species, the ranges of the various races are given on one or more maps. In the distribution section, populations and population trends in individual countries are given where appropriate. A section on breeding follows; for a well-studied species such as the Whinchat this is very comprehensive, covering items such as site fidelity, nest site selection, nest building, egg laying, incubation, clutch size, care and growth of the young, and success rate with notes on predation. Habitat requirements, for both breeding and wintering areas are described very thoroughly, as is the voice (usually with sonograms), food, and movements. There is a detailed section on behavior, often with line illustrations of courtship or aggressive displays, as well as a description of molt. The species accounts end with an up-to-date treatment of the conservation status of each species, which in some cases is a cause for substantial concern.

The information in the individual species accounts is enormously detailed, in fact encyclopedic. The comprehensive bibliography, with some six hundred references, attests to the thoroughness of the author's background research. The only additional information which might have been presented is in the movement section of the two western European species, the Whinchat and the Stonechat (*Saxicola torquata*), for which there is a great body of data arising from the banding schemes of several countries. The movements sections for these two species would have been enhanced by an analysis of banding recoveries, perhaps with maps.

There are 14 color plates, in some cases more than one per species. These are, in a word, superb. They are feather-by-feather accurate, while capturing perfectly the pert, perky nature of the genus. In addition, there are 16 plates of color photographs, with six or more individual photographs per plate, which further add to the visual attraction and comprehensiveness of the book.

In short, *Stonechats* is a major achievement by both author and artist. Because of its exhaustive detail it is not exactly the kind of book one reads cover to cover while snuggled up in front of a warm fire; rather, it clearly will be the standard reference work for the genus for many years to come.—DAVID BREWER.

KANSAS BREEDING BIRD ATLAS. By William H. Busby and John L. Zimmerman. University Press of Kansas, Lawrence. 2001: 466 pp., 381 range maps, 3 tables, 3 appendices. $35.00 (cloth).—This is an outstanding addition to the growing list of state breeding bird atlases. It is comprehensive, easy to use, cleanly printed, well laid out, published in timely fashion, and the data used have been carefully validated.

The book consists of two sections: Introduction, and Species Accounts. The Introduction contains sections on Methods, Geographic Setting, Overview of Results, Species Data, and Guide to the Species Accounts.

The heart of a Breeding Bird Atlas is, of course, the section containing the species accounts. These are well presented, with exceedingly clear atlas block maps for each species, accompanied by a brief but comprehensive and well-written summary of its status as a breeding bird in Kansas. I found these accounts interesting and informative, and along with the maps, they provide a clear picture of a species' breeding distribution. The maps do, however, illustrate a major problem with atlasing in states with few birders: the difficulty of achieving consistent coverage of the entire state. This problem was dealt with in this atlas project by setting out atlas blocks in differing densities across the state. Densest coverage (one block per 6 × 9-mile USGS quadrangle) occurred in the easternmost part of the state, parts of its southwestern and northwestern corners, and the Red Hills region in the south-central part of the state. The rest of the state was divided between two lower densities, one block per 2 quadrangles or one block per 4 quadrangles. According to the authors, this design was predicated on limited availability of personnel and differences in habitat heterogeneity in the state. Although probably unavoidable for these reasons, the resulting range maps for many species at first glance suggest differing densities of occurrence in the state, even when accompanying information indicates even distribution of those species. Thus, the reader must continually keep in mind the areas of the state with the denser atlas block distributions when interpreting the atlas block maps. Illustrative examples are those for the House Sparrow (*Passer domesticus*) and Common Grackle (*Quiscalus quiscula*). In an attempt to correct this problem, the authors have added two tables adjacent to the atlas block map, one that lists the percentage and the other the number of blocks in each physiographic region of the state within which the species was found. These, and a simple additional map titled "Abundance by Stratum" that shows the average number of birds per Breeding Bird Survey (BBS) route within each of the five BBS physiographic strata included in Kansas, do indeed help the reader to overcome the apparent density differences in the atlas block map. The authors themselves suggest that "readers should examine the table of percent frequency of species by physiographic region located in the species accounts."

Within the Introduction, the Methods section contains an outline of the sampling procedure and a list of the breeding codes used in the atlas; the latter follow those recommended by the North American Ornithology Atlas Committee. The authors make an interesting observation: "Fieldwork involved not bird watching, but watching birds," a pithy statement of the requirements of atlasing to which many with birding backgrounds must adjust in order to complete such a project successfully.

Two additional sections of Methods are of critical importance to the integrity of the project: these are titled "Verification and Data Processing" and "Limitations and Biases." It was gratifying to note that submitted data were checked carefully for errors and "validity of the observational details for a certain subset of species that were considered unusual." In Limitations and Biases, the authors deal with the knotty problem of differing densities of atlas blocks throughout the state (discussed above). The authors explain the limitations of the project clearly along with the

steps taken to alleviate these limitations, thus obviating criticism for potential problems that are largely inherent in any atlas project on the Great Plains.

The succeeding sections on Geographic Setting, Overview of Results, and Species Data are well-done discussions with much useful information. Geographic Setting discusses the geography, land use, and habitats of Kansas and presents several clear and useful maps. Sections include Land and Climate, Vegetation and Land Use, Land-Use History, and Physiographic Regions. The Overview of Results is a short section providing statistical information of interest; a block in northeastern Kansas along the Missouri River had the most species reported in any block: 120. The section on Species Data is well done, containing much useful information summarized from the project. Included are tables which show the 20 most frequently reported species in atlas blocks (Mourning Dove, *Zenaida macroura*, and Barn Swallow, *Hirundo rustica*, top the list), and the 20 most frequently confirmed species (Barn Swallow and House Sparrow). Notable also is a segment titled "Biogeographic Patterns," which I consider a significant part of the book. Species are grouped under several headings, a few of which are "Decrease in distribution frequency from south to north," "Peripheral species," and "Southwest distribution." This section points out patterns of distribution that emerged from the atlas data, and is an especially useful tool for those in adjacent states who might be searching for peripheral breeding species in their states.

In summary, I heartily recommend this book to anyone interested in a readable and concise presentation of distributional data for one of the more fascinating Great Plains states. It is well produced and should be a standard work for many years. The authors are to be commended for a job well done.—W. ROSS SILCOCK.

BIRDS IN MISSOURI. By Brad Jacobs. Illustrated by Richard Ferguson, Mark Raithel, and Kristin Williams. Missouri Dept. of Conservation, Jefferson City, Missouri (mdcnatureshop.org). 2001: 375 pp., 17 landscape and habitat illustrations, numerous maps, 216 other figures, and an Appendix. $30.00 (paper), $38.00 (cloth).—When I was a boy, we had only one good choice for a field guide and most of the state bird books had been written shortly after the turn of the century (the one that did not coincide with a millennium change). Today, there are numerous options for field guides and virtually every state has a recent "Birds of" book. With that in mind, *Birds in Missouri* is an interesting mixture of field guide and state bird book, with a bit of ornithology text thrown in on the side. The end result is an attractive package of information and artwork that is very reasonably priced, but one which also does not really fit any of the standard niches in the ornithological literature.

After some introductory material, the book begins with a lovely introduction to the natural vegetation types of Missouri. This is followed by 17 double-page murals that attempt to show the birds typical of the different habitats and landscapes found in Missouri. Each illustration has a map showing where that vegetation occurs in Missouri and some representative locations one could visit to see this set of birds. While the artwork in these is not as professional as most of that in the book, they do a wonderful job of showing how birds are tied to habitats.

The next 250 pages is the field guide portion of the book, where 355 species known to occur regularly in the state are described. Most species have a distribution map, a bar graph showing when the species is in the state, a short descriptive section of text, and an illustration or two. The written material gives brief glimpses into the ecology, songs, and behavior of the species along with its status in Missouri and some hints for identification. The material on identification is not very complete, such that one would not want to replace his or her favorite field guide with this book. The artwork supporting this section is variable in quality, but most of it is highly effective for its purposes. Nearly every group of birds has some additional material, often with illustrations, relevant to that group of birds (e.g., raptors in flight and bird population trends). Also interspersed in this section are 11 two-page spreads on topics varying from the ecology of taxonomic groups (such as humming-

birds and sparrows) to market hunting and wildlife conservation.

The book follows with a 50 page appendix that includes topics ranging from scientific names to birding organizations and has an annotated check-list to Missouri birds. It ends with references, a glossary, indices, and illustration credits.

This is a very nice book that anyone who is interested in birds and lives in Missouri should have. While it is good enough to help identify nearly anything you could reasonably expect to see in Missouri, its 8 1/2 by 11 format precludes its easy use in the field. If you want detailed dates of first or last records or locations for rare sightings, the things a state bird book often gives, you will be disappointed again. On the other hand, if you have seen something at the feeder or in the field and you want to know something more about it, this book provides more information than the usual field guide or state book fare. However, if you just want to sit down, learn more about birds, and look at lots of attractive bird art, *Birds in Missouri* will keep you entertained for hours.—JOHN FAABORG.

BIRD SONG EAR TRAINING GUIDE. By John Feith. John Feith, Madison, Wisconsin. 2003: $14.95 (Audio CD, ISBN 1-932133-09-7).—The *Bird song ear training guide* is a CD that contains the sounds of 189 species of birds that are found in Wisconsin. The sounds are arranged in 95 tracks, and all but the last track contain the sounds of two species. For each species included, the segment includes the sound(s) of the species, a description of the sound and the name of the species, and then a short second opportunity to hear the sound. All the sounds were recorded in Wisconsin or Minnesota and the proceeds from the sale of this recording will benefit the Wisconsin Society for Ornithology and the Nature Conservancy.

My initial response was to question the need for this CD, because the *Birding by ear* series (Richard Walton and Robert W. Lawson. 1989. Peterson Field guide series, Houghton Mifflin, Boston) provides an excellent format for learning bird song and several other CDs also are available for bird sounds. However, as someone who has struggled learning bird song and who works to teach others bird vocalizations, I found this CD to be a very useful resource. Several of the mnemonics that were provided were new and quite useful. For example, describing the Eastern Bluebird (*Sialia sialis*) song as "Cheer, cheerful charmer," the Canada Warbler (*Wilsonia canadensis*) as "chip chip dippety chipety dip," and the Vesper Sparrow (*Pooecetes gramineus*) as "Here here, where where, altogether now" may help me teach these songs to my students. Additionally, this CD included recordings for several species that I did not have on other CDs. For example, the Great Egret (*Ardea alba*) is not included in the *Peterson eastern/central bird songs* (Cornell Lab. of Ornithology, 1990, Houghton Mifflin, Boston) or the *Eastern/central birding by ear* series. Furthermore, the ability to use random play combined with the bird sounds being played before the sound is identified make this CD a nice quiz of bird sounds, particularly during spring when many species are seen in unusual locations during migration.

The *Bird song ear training guide* is organized like an index, so all birds that are called sparrows are together, but the junco is found earlier in the recording. This order is different from either the phylogenetic order or the grouping of similar songs together in other recordings, and is initially a little disconcerting.

Several of the recordings were either quite short (e.g., Boreal Chickadee, *Poecile hudsonicus*, and Common Grackle, *Quiscalus quiscula*) or were not typical of the sounds that I am used to hearing (e.g., Belted Kingfisher, *Ceryle alcyon*, and Purple Martin, *Progne subis*). There is at least one typographic error in the lining notes, which repeated the mnemonic for the Eastern Bluebird for the Eastern Kingbird (*Tyrannus tyrannus*). The use of some adjectives "maniacal" for the Common Loon (*Gavia immer*) and "in pain" for the Ring-billed Gull (*Larus delawarensis*) was somewhat objectionable.

Overall, I found that most of the recordings were of very good quality, the selection of species was extensive and covered many of the species found in midwestern and northeastern states, and the format of bird sounds prior to identification of the species was very useful. I will use this CD both in teaching my

students bird sounds and in preparing for the migrants' return during spring.—SARA R. MORRIS.

WISCONSIN'S NATURAL COMMUNITIES: HOW TO RECOGNIZE THEM, WHERE TO FIND THEM. By Randy Hoffman. Univ. of Wisconsin Press, Madison. 2002: 375 + xiii pp., 16 color figures. $59.95 (cloth), $24.95 (paper).—The author has intended this book primarily for the layman, as scientific names have been excluded from within the text, although the appendix gives both the common and scientific names for those species of mosses, lichens, liverworts, mollusks, snails, and insects not cited in single sources within the text. It truly would have been a more informative volume had the author provided scientific names along with the common names cited throughout the text. Everyone familiar with plants, invertebrates, or vertebrate species knows that common names are very unstable, and vary significantly within regions, and a listing of common and scientific names in a appendix would have served equally as well.

The introduction provides a brief review of the species diversity found within the state of Wisconsin, with insects numbering nearly 40,000 species, while the amphibians and reptiles are lesser represented, with 53 species. Breeding birds number upward of 252 species, and a total of over 400 species are recorded having been sighted within the state of Wisconsin. A comparison of acres of the 28 plant communities found within Wisconsin shows that since the mid-1880s, only the southern red oak mixed forest and dry pine forest habitats have increased in dominance into the late 1900s. All other communities have decreased significantly, with sugar-maple-basswood, mesic prairie, and wet mesic prairie habitats having been drastically affected. As one would easily surmise, agricultural and urban development have been the major cause for natural community destruction.

The author divided the book into two sections, the first describing the natural communities found within the state, and the second describing the 50 sites discussed within the text. Each site is well illustrated with line drawings and maps which depict the specific locality, along with road directions for each community treated within the text. This is followed by a list of noteworthy species of plants, insects, herptiles, birds, and mammals that are noted for the specific area. The author also provides valuable information on population declines for certain species, along with remarks on habitat destruction and its implications, and general information on species to be encountered at different sites. Eight pages of high quality color plates provide a select overview of certain communities and species, although this coverage could easily have been expanded by eliminating some of the line drawings of specific plants and animals throughout the text, which are of little value.

Overall, this excellent book will prove to be a valuable source of information for both professional biologists and laymen alike. I have noted a number of locations which I would like to revisit, along with numerous natural communities which I look forward to seeing. I also would recommend this book to anyone traveling through the state with a general interest in nature as it provides a wealth of information and will certainly make routing a specific trip much more enlightening and productive. Every Wisconsinite should have a copy in his or her home for reference, knowledge, and entertainment.—HARLAN D. WALLEY.

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FRONTISPIECE. Four Golden-crowned Kinglets huddling in the field in a pine tree, 27 December 2002, western Maine. The same postures and positions were retained through the night. (Top) Photograph by B. Heinrich. (Bottom) Dorsal view of the huddling aggregation. Drawing by B. Heinrich.

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OVERNIGHTING OF GOLDEN-CROWNED KINGLETS DURING WINTER

BERND HEINRICH[1]

ABSTRACT.—The Golden-crowned Kinglet (*Regulus satrapa*) is the smallest insectivorous bird that overwinters in boreal forests across North America from Alaska to Nova Scotia, where nights may last 16 h and nighttime temperatures may fall below −40° C. I here provide the first documentation of Golden-crowned Kinglets huddling in the field during winter on open branches. The birds forage until darkness and do not necessarily come back every night to the same site. Traveling in groups and huddling where they end up in the darkness compensates for small body size and potential compromises in foraging time. *Received 28 March 2003, accepted 11 June 2003.*

How 5- to 6-g kinglets can maintain energy balance to survive the long nights at low temperatures has long been an enigma (Ingold and Galati 1997). In winter these birds forage uninterruptedly during the day, feeding predominantly on hibernating caterpillars (Heinrich and Bell 1995). Blem and Pagels (1984) calculated that the fat reserves accumulated during the day in midwinter are insufficient to support endothermy at ambient winter temperatures for an entire night, suggesting that the birds employ torpor, huddle, and/or spend the night in uniquely insulated shelters. However, Reinertsen et al. (1988), working with Goldcrests (*Regulus regulus*) in Austria, found no torpor in captive (presumably well-fed) birds that huddled at night (Thaler 1990) on open branches. Blem and Pagels (1984), on the other hand, saw one Golden-crowned Kinglet (*R. satrapa*) in the wild that apparently entered a squirrel nest.

In the woods of western Maine, the site of the present observations, kinglets routinely travel in mixed species flocks with Black-capped Chickadees (*Poecile atricapillus*), Red-breasted Nuthatches (*Sitta canadensis*), and occasionally Downy Woodpeckers (*Picoides pubescens*) and Brown Creepers (*Certhia americana*). Downy (Kilham 1983) and Hairy (*P. villosus* pers. obs.) woodpeckers excavate holes in fall and winter for shelter during the night, and Red-breasted Nuthatches routinely enter preexisting tree cavities at dusk (pers. obs.). At least one small insectivorous North American bird, the Verdin (*Auriparus flaviceps*) builds winter nests (Walsberg 1990) and therein huddles in groups. The energy consideration of Blem and Pagels (1984) suggested that kinglets may employ some unusual strategy.

In dozens of attempts to follow kinglets during late afternoon and evening, I occasionally was successful in following them for over an hour and until dark, but they always vanished from sight as it was getting too dark to see (i.e., they foraged until after sunset). During early January, 1995, I had on three occasions followed a group of three kinglets at dusk to where I had previously located two red squirrel (*Tamiasciurus hudsonicus*) nests. The birds "disappeared" in a balsam fir (*Abi-*

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es balsamifera) thicket. No kinglets could be flushed from the squirrel nests, nor were any seen to leave them at dawn.

On 19 December, 2000, after a night of heavy winds with driving sleet and snow, I flushed two kinglets in the predawn darkness from near the ground out of a snow-covered brush pile. No kinglets returned to this shelter during the next two evenings.

On 25 November 2002, I saw three kinglets while I was perched about 12 m up in a spruce (*Picea* sp.) tree. As it was starting to get dark (10 min past the official sunset of 16:05 EST) I heard "tsee" calls and then saw a kinglet land on a twig near me. It turned around several times and a second one joined it. The two pressed closely together and then stopped moving. The two then separated briefly after a third bird arrived, but then they rejoined each other to again huddle on the same branch. The third bird called from a dense neighboring balsam fir tree. The two then left their huddle and joined the third one. All three birds then were invisible to me, but several minutes later I heard "tsee" calls from near where they had disappeared from my view into the dense foliage.

The following evening I again first heard and then saw three kinglets in the same area, and they again disappeared into the same dense thicket. I monitored the area for two more nights, occasionally hearing a kinglet but being unable to follow one. This site contained a red squirrel nest. On each of the four evenings, the squirrel returned to its nest about 30–60 min before the kinglets arrived. I watched the nest closely but did not see any kinglets enter it.

On the evening of 27 December 2002, at 16:20 (after the sun was below the horizon but it was not yet dark) I saw three kinglets fly into a brushy white pine (*Pinus strobus*). In less than a minute I found four kinglets huddled together about 4 m above the ground under thick branches. I returned an hour later and from a step ladder examined the birds in the beam of a flashlight. The birds' chests were pointing inward and their tails pointing outward in three directions. The birds showed no reactions to repeated photographic flashes from a distance of 20 cm (Fig. 1) and their heads remained fully tucked into the back feathers. One bird jerked its head up when I jiggled the roost, and then just as quickly retracted it back into its fluffed out feathers. Temperatures then were −4° C, but later that night declined to −10° C. I again checked the birds at 19:30 and in the predawn at 04:30. As before, the tail positions had not shifted and rapid breathing movements were visible; the birds apparently were not in torpor. No birds were seen at that site during the next week.

Hundreds of observations of Golden-crowned Kinglets during winter in western Maine indicated that these birds always traveled in groups of two to four. The kinglets commonly join up with chickadee flocks, but separate from them in the evening.

The present observations indicate that although microhabitats for nocturnal roosts are likely important, overnighting sites may be less specific and less important than the ability to huddle quickly. Overwintering Golden-crowned Kinglets apparently do not generally return to the same site each night. Instead, they forage until nightfall and huddle tightly near where they end up.

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THE NEST AND EGGS OF THE CINEREOUS MOURNER (*LANIOCERA HYPOPYRRA*)

GUSTAVO A. LONDOÑO[1] AND CARLOS DANIEL CADENA[2,3]

ABSTRACT.—We present the first account of nesting biology for the Neotropical suboscine genus *Laniocera* by describing the nest and eggs of the Cinereous Mourner (*L. hypopyrra*) based on observations made in the Peruvian Amazon during 2001. The cup-shaped nest was in mature floodplain forest among the branches of an epiphytic fern in a small tree 1.8 m above the ground, and contained two buffy eggs with chocolate brown blotches and spots. These observations demonstrate that *Laniocera* is not a cavity nester, supporting its removal from the myiarchine flycatchers and previous suggestions of a close relationship to the genus *Schiffornis*. *Received 12 December 2002, accepted 12 March 2003.*

The tyrannoid genus *Laniocera* includes two Neotropical lowland forest species, the Speckled Mourner (*L. rufescens*), found from southeastern Mexico to northwestern Ecuador, and the Cinereous Mourner (*L. hypopyrra*), found throughout Amazonia and in the Atlantic forests of Brazil (Ridgely and Tudor 1994). Based on a variety of morphological characters, *Laniocera* is placed within the monophyletic *Schiffornis* group, an assemblage of uncertain systematic affinities that also includes the genera *Schiffornis*, *Laniisoma*, *Iodopleura*, *Xenopsaris*, and *Pachyramphus* (Prum and Lanyon 1989). In addition to Prum and Lanyon's (1989) morphological study, two different analyses of DNA sequences with incomplete taxon sampling (both lacking *Laniocera*) have supported the monophyly of the *Schiffornis* group, expanding it to include *Tityra* (Prum et al. 2000, Johansson et al. 2002).

Prum and Lanyon (1989) pointed out that despite insufficient information, it is apparent that the genera in the *Schiffornis* group are very diverse behaviorally and ecologically, and represent an impressive radiation in breeding systems, parental care, nest construction, and habitat. This would make this group particularly interesting for inclusion in comparative studies on the evolution of alternative reproductive behaviors and life history strategies in birds (Bennett and Owens 2002). However, this has not been possible because the natural history of many of the species in the assemblage remains very poorly known. Particularly, the nests of two of the genera (*Laniocera* and *Laniisoma*) have not been described previously.

Based on observations made in a lowland rainforest site in the Peruvian Amazon, here we present the first data on nesting biology for the genus *Laniocera* by describing the nest and eggs of the Cinereous Mourner (*L. hypopyrra*). Since nesting biology can be informative about phylogenetic relationships in birds (Sheldon and Winkler 1999, Zyskowski and Prum 1999), we compare the nest and eggs of *L. hypopyrra* with those of other genera in the *Schiffornis* group, and of other suboscines with which *Laniocera* had been grouped in the past.

STUDY SITE

We made our observations at Cocha Cashu Biological Station, an area of undisturbed lowland forest located in the meander belt of the Manu River in Manu National Park, Dep. Madre de Dios, southeastern Peru (11° 54′ S, 71° 18′ W; about 400 m elevation). The station encompasses a variety of vegetation types; our observations took place in mature floodplain forest, which occupies the greater part of the meander belt (Terborgh 1983). This habitat is characterized by multiple strata including a 25- to 30-m tall canopy broken by emergent trees of 50–60 m height. Palms are common and diverse both in the canopy and understory. The understory is relatively open and composed especially of plants in the Rubiaceae, Melastomataceae, Nyctaginaceae, and Myrsinaceae. The ground is covered by *Tectaria incisa* ferns, which are replaced by

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FIG. 1. Nest of the Cinereous Mourner (*Laniocera hypopyrra*) found at Cocha Cashu Biological Station, Peruvian Amazon, 30 September 2001. Photograph by Gustavo A. Londoño.

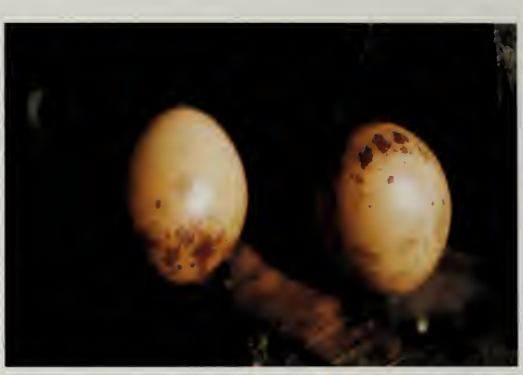

FIG. 2. Eggs of the Cinereous Mourner (*Laniocera hypopyrra*) found at Cocha Cashu Biological Station, Peruvian Amazon, 30 September 2001. Photograph by Gustavo A. Londoño.

Heliconia spp. in places where there is standing water. Most of the approximately 200 cm of annual rain falls between November and May; monthly rainfall from June through October typically is <10 cm (Terborgh 1990).

Within the study area, the Cinereous Mourner is restricted mostly to the mature phase of the primary successional gradient that results from the river's dynamics (Robinson and Terborgh 1997), but singing males also can be found in earlier successional vegetation (GAL unpubl. data). The species is relatively rare at Cocha Cashu, occurring at low densities of 1–2 individuals per 100 ha in the floodplain forest (Robinson and Terborgh 1997, Terborgh et al. 1990).

NEST DESCRIPTION

An active nest of the Cinereous Mourner was found by J. Tobias in mature floodplain forest on 29 September 2001, a time of the year of generalized breeding activity at Cocha Cashu (Terborgh et al. 1990). The nest was in a small tree (about 4 m tall and 2.4 cm dbh) located in a relatively open area with little vegetation cover in the understory and no tall, woody plants within 2 m. The nest, an unlined bulky cup made of dry leaves, was constructed among the branches of an epiphytic fern which was attached to the tree's trunk 1.8 m above the ground (Fig. 1). The nest dimensions were: depth 74 mm, inner cup diameter 94 × 98 mm, and outer diameter 100 × 160 mm. The walls of the upper part of the nest were very thin, consisting of a single layer of leaves. When found, the nest contained two buff eggs with somewhat longitudinally elongated chocolate brown blotches with underlying light brown markings concentrated on the wider end, and small brown spots scattered throughout (Fig. 2). The eggs measured 28 × 21.5 mm and 28 × 22 mm; each weighed 6.25 g.

Our observations of the nest were limited because it was located far from the station. During two visits we observed only one individual attending the nest. Based on the presumed lek mating system of the species (Prum and Lanyon 1989) and female-only incubation in other behaviorally known members of the *Schiffornis* clade (Skutch 1969), this bird likely was a female, but this could not be confirmed due to the lack of sexual dimorphism. The incubating bird(s) clearly showed the characteristic cinnamon rufous spots in the

wings, which distinguish the Cinereous Mourner from otherwise similar species that occur in the study area (i.e., Screaming Piha *Lipaugus vociferans* and Grayish Mourner *Rhytipterna simplex*). Both eggs disappeared from the nest by 6 October, probably due to predation.

DISCUSSION

The systematic position of *Laniocera* has been uncertain; the genus has been placed variously in the Cotingidae, Pipridae, and Tyrannidae (Prum and Lanyon 1989). Based on morphological features of the nasal capsule and the syrinx, Lanyon (1985) concluded that *Laniocera* is not a near relative of *Myiarchus* flycatchers as had been suggested by Ames (1971), and recommended removing it from the subfamily Tyranninae. However, some uncertainty has remained regarding the affinities of *Laniocera* to the flycatchers (see Ridgely and Tudor 1994, Ridgely and Greenfield 2001). An additional shared derived trait defining the myiarchine flycatchers is that they obligatorily nest in tree cavities (Lanyon 1985); thus, Ridgely and Tudor (1994) suggested that nesting information for *Laniocera* would be of interest to help establish its relationships. Our observations show that *Laniocera* is not a cavity nester like the myiarchines, and thus give further support for its removal from the group.

At a higher level, the systematic position of *Laniocera* and its near relatives (i.e., the *Schiffornis* group) within the superfamily Tyrannoidea is unclear, and they are listed as *Incertae sedis* by the American Ornithologists' Union (1998). Prum et al. (2000) suggested that the *Schiffornis* group, including *Tityra*, should be considered a subfamily (Tityrinae) of the Cotingidae, a suggestion tentatively accepted by the South American Checklist Committee of the American Ornithologists' Union as of March 2003, with a final decision awaiting further evidence (J. V. Remsen pers. comm.). Nests and eggs of *Laniocera* and other members of the *Schiffornis* group (Prum and Lanyon 1989, see below) are not unlike those of many Cotingidae, which build simple open cup or saucer-shaped nests and lay buff, khaki, or olive eggs with spots and blotches of darker browns, sepia, and/or ashy violet colors (Snow 1982).

Within the *Schiffornis* group, three morphological synapomorphies support the placement of *Laniocera* and *Laniisoma* as sister taxa, and two more suggest *Schiffornis* is sister to the *Laniisoma-Laniocera* clade (Prum and Lanyon 1989). Somewhat different relationships are suggested by the molecular phylogeny of Prum et al. (2000), but the conflicting nodes are not well supported and are unstable to different character weighting schemes. Within the clade, the bulky open cup nest of the Cinereous Mourner contrasts with the globular nests with side or bottom entrance of *Pachyramphus* (Skutch 1969), the small and tidy cups of cobwebs and fungus fibers of *Iodopleura* (Snow 1982), the loose nests placed in tree cavities of *Tityra* (Skutch 1969), and the compact open cups of fine dry grasses, fibers, and spider webs of *Xenopsaris* (Smith 1971, Di Giacomo and Leiberman 2000). Conversely, the nest is quite similar to that of the Thrush-like Schiffornis (*Schiffornis turdinus*), which builds a large, bulky cup of dry leaves and leaf skeletons lined with dark rhizomorphs in the crotch of a tree or in a clump of vegetation against a tree trunk within 2 m from the ground (Skutch 1969, Stiles and Skutch 1989). Moreover, the color and pattern of the eggs of *S. turdinus* (pale buffy with blotches and roundish spots of black and dark brown or black and pale lilac concentrated around the wider end; Skutch 1969) fit well with our observations for *Laniocera hypopyrra*. However, eggs of other tyrannoids not immediately related to the *Schiffornis* group (e.g., *Rupicola*, some *Tyrannus*) have similar color patterns, whereas eggs of other putative members of the group (*Iodopleura*, *Xenopsaris*) are different, which suggests this character cannot always be used reliably to establish relationships. Notwithstanding, assuming that the similarities in nest shape, placement, and materials reflect homology, these argue for a close relationship between *Laniocera* and *Schiffornis*, supporting the hypothesis proposed by Prum and Lanyon (1989) based on morphological data. Nests of other taxa that belong in this clade (*Laniisoma*, *Laniocera rufescens*, *Schiffornis major*, and *S. virescens*) remain undescribed, but these appear to share with *Laniocera hypopyrra* and *Schiffornis turdinus* a derived polygynous mating system in which males sing in loose, small leks and are

emancipated from parental care (Prum and Lanyon 1989, Stiles and Skutch 1989).

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NESTING ECOLOGY OF MIXED-GRASS PRAIRIE SONGBIRDS IN SOUTHERN SASKATCHEWAN

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ABSTRACT.—During 1996–2000, I studied the nesting ecology of Sprague's Pipits (*Anthus spragueii*), Clay-colored Sparrows (*Spizella pallida*), Savannah Sparrows (*Passerculus sandwichensis*), Baird's Sparrows (*Ammodramus bairdii*), Chestnut-collared Longspurs (*Calcarius ornatus*), and Western Meadowlarks (*Sturnella neglecta*) on 47 native mixed-grass prairie pastures in southern Saskatchewan. Predation was the primary cause of nest failure and occurred at a similar frequency among the six species. Nest success and productivity varied among years and was lowest during 1997, the year of a substantial increase in meadow vole (*Microtus pennsylvanicus*) populations in southern Saskatchewan. Nest predation was most severe during the nestling stage with daily survival rates typically lower than those of the incubation period. Brown-headed Cowbirds (*Molothrus ater*) parasitized nests of all six species, with 5–29% of host nests containing cowbird eggs. Savannah Sparrows, Clay-colored Sparrows, and Western Meadowlarks incurred the highest frequency of brood parasitism. Parasitized hosts experienced lower productivity due to a combination of reductions in clutch size, hatching success, and fledging success. Overall, brood parasitism by cowbirds cost these birds between 1.3 and 2.2 young per successful nest. These results support the general contention that nest predation is the primary factor influencing grassland songbird reproductive success. *Received 10 December 2002, accepted 12 March 2003.*

The nesting ecology of grassland songbirds in the northern mixed-grass prairie has received little attention, partly because of the perceived and real difficulty in locating nests (Bent 1950, Lane 1968). Subsequently, our ability to adequately identify proximate and ultimate factors contributing to the widespread population declines of grassland birds (Sauer et al. 2001) often is limited because we lack basic information on many aspects of their breeding ecology, particularly factors influencing their reproductive success. Sprague's Pipit (*Anthus spragueii*), for example, is listed as a threatened species (Committee on the Status of Endangered Wildlife in Canada 2000), and has been described as one of North America's least-known birds (Robbins and Dale 1999). Although several recent studies have examined habitat use in northern grassland songbirds (Dale et al. 1997, Sutter and Brigham 1998, Davis et al. 1999, Madden et al. 2000, Johnson and Igl 2001, McMaster and Davis 2001), only Maher (1973), Koford (1999), and Davis and Sealy (2000) have reported on aspects of the breeding biology and factors reducing nest success of this songbird community. Other studies in the northern Great Plains have involved single species (Knapton 1978, Hill 1997, Davis and Sealy 1998), or have focused on only brood parasitism (Koford et al. 2000), making demographic comparisons within and among grassland bird communities difficult.

Nest predation and brood parasitism often are cited as the primary factors responsible for lowering reproductive success of grassland songbirds. Martin (1993) showed that grassland species typically experience higher rates of nest predation than birds nesting in forest and wetland habitats. Although nest success varies regionally, recent studies indicate that as many as 70% of grassland bird nests are destroyed by predators (Patterson and Best 1996, Best et al. 1997, Winter 1999, Davis and Sealy 2000). Brown-headed Cowbirds (*Molothrus ater*) also may lower reproductive success by removing host eggs and out competing host nestlings for food and space (Payne 1977). However, as with nest predation, the frequency and impact of brood parasitism on grassland hosts vary geographically. Robinson et al. (2000) found that grassland hosts in Illinois experienced parasitism frequencies of <5%, whereas parasitism frequencies in other regions often were >30% (Koford et al. 2000). In this paper I quantify the extent of nest predation and brood parasitism and compare aspects of the nesting ecology of six grassland songbirds in native

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mixed-grass prairie pastures in southern Saskatchewan, Canada.

METHODS

Study area.—I conducted the study on native pastures in the eastern portion of the mixed- and moist mixed-grassland ecoregions of southern Saskatchewan (49° 45′ N, 105° 45′ W; see Davis et al. 1999 for a description of the region) during the 1996–2000 nesting seasons. I selected pastures in fair-to-good range condition under light-to-moderate grazing intensity (Task Group on Unity in Concepts and Terminology 1995) to increase the likelihood of locating nests of high conservation priority species such as Baird's Sparrow (*Ammodramus bairdii*) and Sprague's Pipit, and to ensure similar breeding bird communities among sites. A different set of pastures was selected for most years of the study for a total of 47 pastures on which nests were located (8 pastures during 1996, 12 during 1997, 10 each during 1998 and 1999, and 7 during 2000). Native pastures were flat to gently rolling and the vegetation consisted predominantly of *Stipa* spp., June grass (*Koeleria macrantha*), northern wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), sedges (*Carex* spp.), club moss (*Selaginella densa*), sage (*Artemisia* spp.), and various other forbs. Common shrubs were western snowberry (*Symphoricarpos occidentalis*) and rose (*Rosa* spp.).

Nest searches.—Nest searching and monitoring were conducted from early May to early August each year. Nests were located mostly between 07:30 and 14:00 CST by flushing adults from their nests with a 25-m nylon rope weighted with aluminium and tin cans attached every 0.5 m. Nests also were located fortuitously on the pastures throughout the day. Nests were marked with color surveyor flags and bamboo stakes placed 5 m away and monitored every 2–5 days until the young fledged or the nesting attempt failed. Eggs were candled (Lokemoen and Koford 1996) to determine clutch initiation dates and to estimate hatching dates for increased accuracy in calculating survival rates (Mayfield 1975). Nest attempts were considered successful if at least one host nestling survived to fledging age (i.e., left the nest), except when comparing parasitized and nonparasitized nests for which successful nests included nests fledging at least one host or cowbird young. Cues such as adult(s) uttering alarm calls nearby, nestling age on previous visit, minimal nest disturbance, fledglings in the vicinity of the nest, and the presence of feces and feather scales in the nest were used to identify successful nests.

Statistical analyses.—I conducted all analyses using SAS ver. 8 (SAS Institute, Inc. 1999). I used the median test (PROC NPAR1WAY) to determine whether median clutch initiation dates differed among years for each species. Clutch initiation dates from 1996 were not included in this analysis, as eggs were not candled during that year. To determine whether host clutch size changed as the breeding season progressed, I calculated the mean clutch size during each week and regressed the mean clutch size as a function of week using the square root of the number of nests as a weighting factor. Weekly periods that comprised only one nest were excluded from analyses. I calculated daily survival rates using the Mayfield method (Mayfield 1961, 1975) with standard errors as per Johnson (1979). I used only the incubation and nestling periods to calculate nest success. The halfway point between the last visit when the nest was active and a subsequent visit was used to calculate the number of exposure days for nests with known fate. For nests whose fates were uncertain, I included exposure days only up to the last visit that the nest was active (Manolis et al. 2000). I compared daily survival rates during the incubation and nestling periods using Johnson's (1979) methodology. I used one-way ANOVA and least squares means, weighted by the square root of exposure days for each year, to determine whether daily survival rates differed among years. I used pastures as sample units to avoid pseudoreplication (Hurlbert 1984) as individual nests within a pasture likely are not independent. I used the same analyses to determine whether productivity differed among years, except that I used the square root of the number of nests as a weighting factor. I compared clutch size, hatching success, and productivity of parasitized and nonparasitized nests using Student's *t*-tests (PROC TTEST).

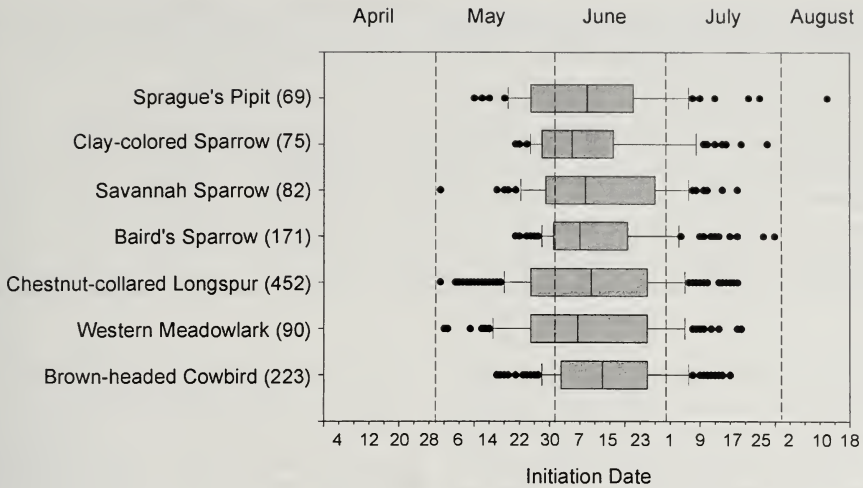

FIG. 1. Peak egg laying occurred during the first two weeks of June for grassland songbirds in southern Saskatchewan, 1997–2000. Number of nests or cowbird eggs are in parentheses. Box plots represent 25th, 50th, and 75th percentiles; whiskers indicate 10th and 90th percentiles; and dots are outliers.

RESULTS AND DISCUSSION

Overall, 1,300 nests of 27 species were located over the five years of the study. Most nests were passerines (n = 1,083), followed by waterfowl (n = 150), shorebirds (n = 59), and grouse (n = 5), along with two Common Nighthawk (*Chordeiles minor*) nests and one Short-eared Owl (*Asio flammeus*) nest. This paper focuses on the six songbird species that composed 80% of the total number of nests: Chestnut-collared Longspur (*Calcarius ornatus*, n = 500), Baird's Sparrow (n = 184), Western Meadowlark (*Sturnella neglecta*, n = 111), Savannah Sparrow (*Passerculus sandwichensis*, n = 88), Clay-colored Sparrow (*Spizella pallida*, n = 85), and Sprague's Pipit (n = 67).

Clutch initiation.—The peak of clutch initiation occurred within the first two weeks of June for most songbirds (Fig. 1). Western Meadowlarks and Chestnut-collared Longspurs typically initiated nests earlier, and Baird's and Clay-colored sparrows nested later in the breeding season. Initiation dates are consistent with typical arrival times of these species. During 1995–2002 in Saskatchewan, Western Meadowlarks and Chestnut-collared Longspurs usually arrived during the first and third weeks of April, respectively, whereas Baird's and Clay-colored sparrows arrived during the first two weeks of May (unpubl. data). Savannah Sparrows and Sprague's Pipits typically arrived in late April to early May. Davis (1994) found a similar pattern in the breeding phenology of grassland birds in southwestern Manitoba. Median clutch initiation dates differed significantly among years for Chestnut-collared Longspurs (χ^2 = 21.49, df = 3, $P < 0.0001$) and Western Meadowlarks (χ^2 = 8.19, df = 3, P = 0.042) and tended to differ among years for Sprague's Pipits (χ^2 = 6.68, df = 3, P = 0.080). Longspurs and pipits initiated nests later in 1997 than in subsequent years, whereas meadowlarks initiated nests earlier in 1997 and 1999 than in other years. Longspurs arrived a week later in 1997 (5 May) compared to 1996 (28 April) and more than two weeks later than in 1998–2000 (17–19 April). The variation in laying phenology of pipits and meadowlarks, however, did not appear to be influenced by arrival dates, as arrival dates were similar for all years.

Clutch size.—Clutch sizes of all species (Table 1) fell within the range of those reported previously (Wheelright and Rising 1993, Knapton 1994, Lanyon 1994, Sutter 1996, Hill and Gould 1997, Davis and Sealy 1998). Baird's Sparrows, Savannah Sparrows, and Sprague's Pipits typically laid four or five eggs whereas Clay-colored Sparrows and Chestnut-collared Longspurs mostly laid four-egg clutches. Five- and six-egg clutches were most commonly observed in Western Mead-

TABLE 1. Clutch sizes of six grassland songbirds nesting in southern Saskatchewan, 1996–2000.

Species	Clutch size (%)					
	2	3	4	5	6	Mean ± SE
Sprague's Pipit (n = 57)	1 (1.7)	1 (1.7)	18 (31.6)	26 (45.7)	11 (19.3)	4.8 ± 0.11
Clay-colored Sparrow (n = 57)	0	10 (17.5)	46 (80.7)	1 (1.8)	0	3.8 ± 0.05
Savannah Sparrow (n = 61)	1 (1.6)	3 (5.0)	28 (45.9)	28 (45.9)	1 (1.6)	4.4 ± 0.09
Baird's Sparrow (n = 146)	0	6 (4.1)	52 (35.6)	88 (60.3)	0	4.6 ± 0.05
Chestnut-collared Longspur (n = 414)	7 (1.7)	52 (12.6)	227 (54.8)	122 (29.5)	6 (1.4)	4.2 ± 0.03
Western Meadowlark (n = 73)	0	5 (6.8)	10 (13.7)	33 (45.2)	25 (34.3)	5.1 ± 0.10

owlark nests. A quadratic relationship best described Baird's Sparrow and Chestnut-collared Longspur clutch size as a function of week whereas Western Meadowlark clutch size decreased as the breeding season progressed (Fig. 2). Savannah Sparrow clutch size tended to decrease with the breeding season (t = −2.14, df = 8, P = 0.069) while Sprague's Pipit clutches tended to be largest midway through the breeding season ($F_{2,6}$ = 3.76, P = 0.087). Clutch size of Clay-colored Sparrows did not vary significantly as the breeding season progressed ($F_{2,4}$ = 0.93, P = 0.46). Previous studies have reported decreasing clutch sizes during the breeding season for Western Meadowlarks and Savannah Sparrows (Lanyon 1957, Dixon 1978, Wray et al. 1982), although Dickinson et al. (1987) found only a weak relationship for meadowlarks. Maher's (1973) observations that Sprague's Pipit and Chestnut-collared Longspur clutches initiated in June tended to be larger than those initiated in May or July are consistent with my results. Davis and Sealy (1998) found that Baird's Sparrows typically laid larger clutches earlier in the breeding season. Smaller clutches earlier in the season for some species may reflect lower metabolic resources due to energetic demands during migration and lower prey abundance during early summer, whereas reduced metabolic resources later in the season may result from renesting and double brooding (Wray et al. 1982).

Nest success and productivity.—Nest predation was the major cause of reproductive failure, with nest desertion and other causes of nest failure accounting for a small proportion of unsuccessful nests (Table 2). Overall, predation accounted for 88% of unsuccessful nests, which is comparable to rates reported for grassland songbirds in other regions (Wray et al. 1982, Davis 1994, Knapton 1994, Hill and Gould 1997, Winter 1999, S. L. Jones unpubl. data). Apparent nest success, predation, and productivity were similar among species, although Clay-colored Sparrows were least successful, due to a combination of higher frequencies of desertion and nest failure unrelated to predation (i.e., inclement weather and cattle activity). Hatching success for the six species ranged between 55 and 63%, and of the eggs incubated full term, 65–77% hatched (Table 2).

Daily survival rates were higher during the incubation period than during the nestling period for all species, although differences were not significant ($P > 0.10$ in all cases). S. L. Jones (unpubl. data) found that survival was higher during the incubation stage for six of seven grassland songbird species studied in Montana, and Davis (1994) found a similar pattern for four of six species in Manitoba. Patterson and Best (1996) also reported higher survival rates during the incubation period for four of five species breeding in Iowa, whereas Winter (1999) found that survival of Dickcissel (*Spiza americana*) nests in Missouri was lower during the incubation period and found no difference in egg and nestling survival in Henslow's Sparrows (*Ammodramus henslowii*). The lower survival rates during the nestling period may be due to predators cuing in on the increased activity of adults feeding young and nestlings begging for food (Haskell 1994), although this likely depends upon the composition of the predator community (i.e., predators relying primarily on visual instead of auditory cues) and parental behavior (Halupka 1998).

Mayfield nest success ranged from 13.9% for Clay-colored Sparrows to 24.0% for Sprague's Pipits (Table 3). Davis and Sealy

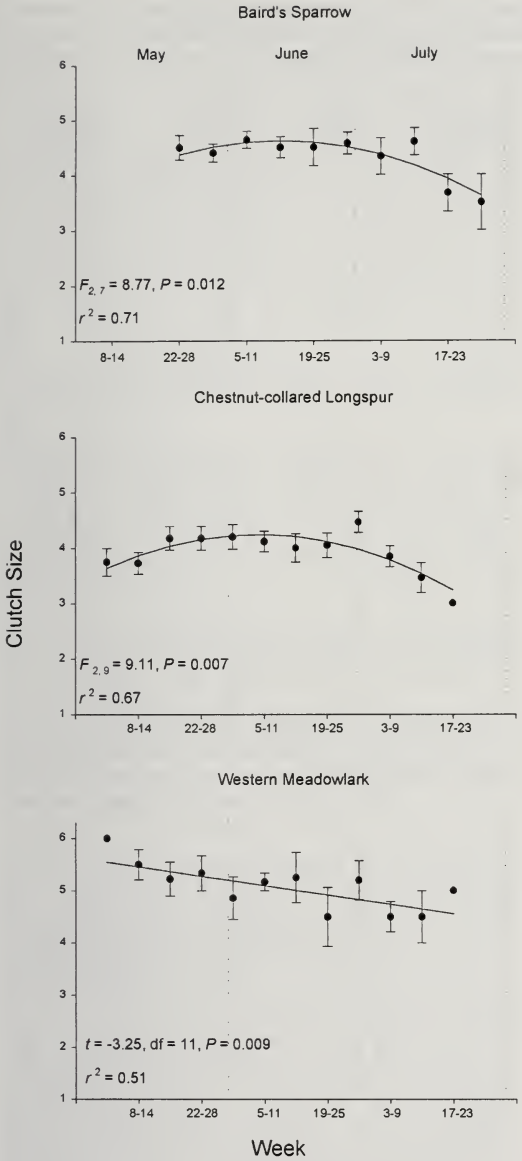

FIG. 2. Clutch size varied with breeding season for three grassland songbirds in southern Saskatchewan, 1997–2000. Values are means ±SE.

(2000) reported lower nest success rates for most species in a similar bird community in southwestern Manitoba, although nest success for Chestnut-collared Longspurs in Manitoba was higher (30%) compared to Saskatchewan (21.6%). Similarly, in Montana, nest success rates were 4–11% higher for similar species over the same period (S. L. Jones unpubl. data). The low success rates I observed were due mainly to poor nest success during 1997 (Fig. 3), particularly for Sprague's Pipits ($F_{3,18}$ = 7.39, P = 0.002) and Baird's Sparrows ($F_{4,31}$ = 6.04, P = 0.001). This likely was related to a substantial increase in meadow vole (*Microtus pennsylvanicus*) populations that occurred over a large region of southern Saskatchewan (Poulin et al. 2001), whereas no such phenomenon occurred in Montana (S. L. Jones pers. comm.). With the 1997 data removed, nest success estimates increased to 24–32%, which is comparable to those found in Montana. Interestingly, the low nest success during 1997 may be attributed mainly to lower survival during the nestling stage. Daily survival rates during the incubation period did not differ significantly among years (P > 0.25), whereas nestling daily survival rates differed among years for Savannah Sparrows ($F_{4,20}$ = 2.70, P = 0.060) and Sprague's Pipits ($F_{3,17}$ = 13.06, P = 0.0001); nestling daily survival rates were lowest during 1997 and 1998 for Savannah Sparrows and lowest during 1997 for Sprague's Pipits. Temporal variation in nest predation has been linked to vole populations in other regions. Bientema and Muskens (1987), for example, found that nest success of shorebirds was related to the amount and direction of changes in vole densities. Nest predators appeared to shift to bird nests following a collapse in vole populations. Although nest success of large birds may be relatively high during years when voles are abundant because predators switch from bird nests to voles, voles may lower nest success of songbirds directly by depredating their nests (Bures 1997). It is unknown whether voles were directly responsible for increased nestling mortality in this study or whether the increased mortality was due to higher rates of incidental predation resulting from increased number of predators responding to the voles.

The low nest success during 1997 resulted in relatively low productivity for Baird's Sparrows ($F_{4,39}$ = 3.23, P = 0.022), Sprague's Pipits ($F_{3,23}$ = 5.36, P = 0.006), and Western Meadowlarks ($F_{4,36}$ = 3.16, P = 0.025; Fig. 4). The mean number of host young fledged by Baird's Sparrows was lower during 1997 and 1998 than during 1999 or 2000, and the productivity of pipits was highest during 1999. Meadowlarks fledged significantly more young in 1996 than during 1997–1999. The

TABLE 2. Apparent nest success, hatching success, and productivity of six grassland birds in southern Saskatchewan, 1996–2000. Sample sizes represent the number of nests with known outcomes for each species.

Species	Sprague's Pipit (n = 65)	Clay-colored Sparrow (n = 79)	Savannah Sparrow (n = 80)	Baird's Sparrow (n = 167)	Chestnut-collared Longspur (n = 474)	Western Meadowlark (n = 95)
Percentage of nests successful[a]	30.8	20.3	27.5	25.8	29.5	29.5
Percentage of nests depredated	55.4	60.8	61.3	62.9	64.4	64.2
Percentage of nests deserted	9.2	8.9	3.8	5.4	1.7	1.0
Percentage of nests failed	4.6	10.1	7.5	6.0	4.4	5.3
Percentage of eggs hatched (n)	55.1 (55)	61.6 (53)	63.0 (55)	59.5 (132)	58.9 (390)	55.1 (65)
Percentage of eggs incubated full term that hatched (n)	64.9 (46)	71.4 (45)	76.9 (45)	75.4 (103)	76.6 (299)	68.5 (52)
Host young fledged/nest	1.0 ± 0.22	0.6 ± 0.14	0.8 ± 0.17	0.9 ± 0.13	0.9 ± 0.07	1.0 ± 0.17
Host young fledged/successful nest (n)	3.4 ± 0.32 (20)	3.0 ± 0.24 (16)	3.0 ± 0.26 (22)	3.4 ± 0.19 (43)	3.0 ± 0.10 (141)	3.4 ± 0.22 (29)

[a] Fledged at least one host young.

number of young fledged per successful nest varied among years for Baird's Sparrow and Western Meadowlark ($F_{4,21} = 2.47$, $P = 0.076$ and $F_{4,17} = 4.53$, $P = 0.011$, respectively; Fig. 4). Baird's Sparrow nests fledged more young from successful nests during 1999 than 1996 or 1997, and Western Meadowlarks fledged the fewest young in 1997.

Overall, grassland songbirds in Saskatchewan fledged between 0.6 and 1.0 young per nest and between 3.0 and 3.4 young from successful nests (Table 2). As with nest success, S. L. Jones (unpubl. data) reported higher fledging rates in Montana (1.2–1.7 host young/nest), but the number of host young fledged from successful nests (2.9–3.5) was similar to what I observed.

Cowbird parasitism.—The median egg-laying dates for Brown-headed Cowbirds did not differ significantly among years ($\chi^2 = 4.43$, df = 3, $P = 0.22$). Overall, the cowbird egg-laying season extended from 16 May to 17 July and peaked during the second week of June. Although some host nests were initiated before or after the cowbird laying season, most nests were available to cowbirds throughout the breeding season (Fig. 2). Parasitism frequency varied among years for Chestnut-collared Longspurs ($\chi^2 = 44.31$, df = 4, $P < 0.0001$), Savannah Sparrows (Fisher's Exact Test, $P = 0.053$), and Western Meadowlarks (Fisher's Exact Test, $P = 0.001$). Longspurs were parasitized more frequently during 1996 (50%) than during subsequent years (9–18%), whereas Savannah Sparrows and Western Meadowlarks were parasitized most frequently during 1996 (40 and 50%, respectively) and 1997 (45 and

TABLE 3. Mayfield nest success and daily survival rates (DSR ± SE) for incubation and nestling periods of six grassland songbirds in southern Saskatchewan, 1996–2000.

Species	Incubation period (days)	Nestling period (days)	Number of nests	Incubation DSR	Nestling DSR	Nest success (%)
Sprague's Pipit	13	11	65	0.944 ± 0.011	0.940 ± 0.013	24.0
Clay-colored Sparrow	11	9	84	0.925 ± 0.014	0.883 ± 0.018	13.9
Savannah Sparrow	11.5	9	84	0.952 ± 0.010	0.903 ± 0.015	22.7
Baird's Sparrow	11.5	9.5	182	0.949 ± 0.007	0.906 ± 0.011	21.7
Chestnut-collared Longspur	11.5	10	493	0.943 ± 0.004	0.918 ± 0.006	21.6
Western Meadowlark	13	11	104	0.943 ± 0.010	0.923 ± 0.012	19.2

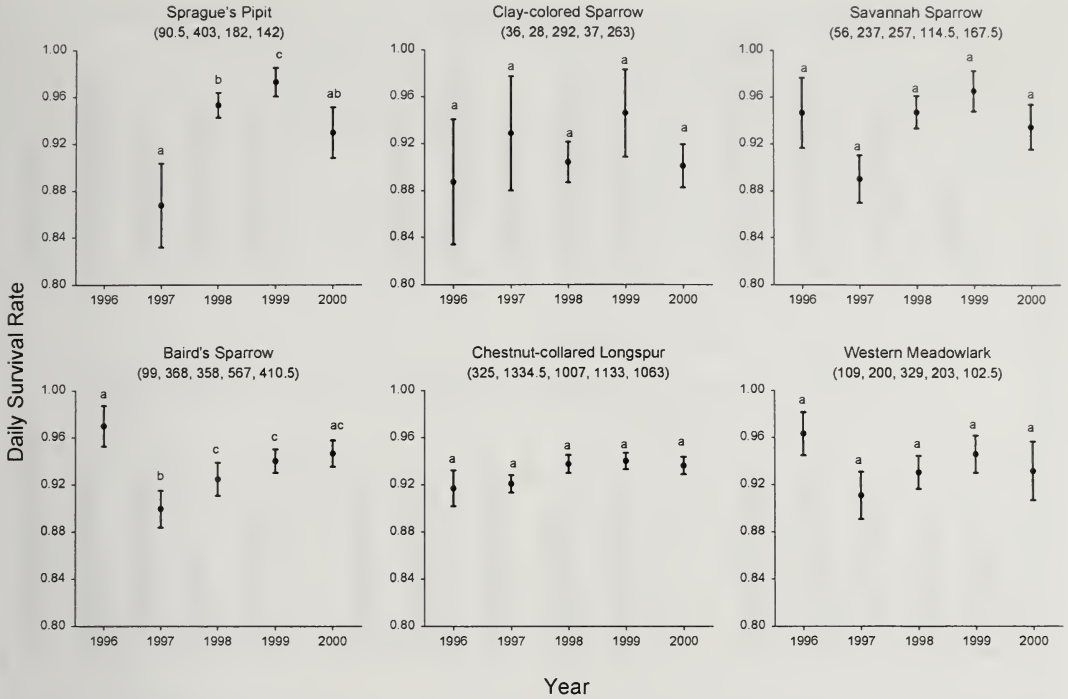

FIG. 3. Annual variation of mean (± SE) daily survival rates (incubation and nestling period combined) for six grassland songbirds in southern Saskatchewan, 1996–2000. Exposure days are in parentheses for each year. Years sharing the same letter do not differ significantly ($P > 0.05$, one-way ANOVA) from each other. No Sprague's Pipit nests were found in 1996.

42%, respectively) than during other years (6–23%). Savannah Sparrow and Western Meadowlark nests were not parasitized during 1999 and 2000, respectively. It is unknown whether variations in parasitism frequencies were linked to cowbird density, as cowbird densities were not quantified in 1996 and 1997.

Overall, cowbirds parasitized 15–29% of host nests in this study (Table 4). Savannah Sparrow, Clay-colored Sparrow and Western Meadowlark incurred the highest frequency of parasitism. The infrequent parasitism recorded for Sprague's Pipit and Chestnut-collared Longspur nests in this study is consistent with that found in Manitoba (Davis and Sealy 2000) and Montana (S. L. Jones unpubl. data). Although egg ejection by cowbird hosts could account for the low parasitism frequencies I observed, there are no published data on egg rejection behavior in Sprague's Pipits. However, Davis et al. (2002) found that the low parasitism frequency reported for longspurs (see Hill and Gould 1997) was not due to egg rejection. Instead, the authors suggested that other antiparasite strategies (e.g., nest defense behavior) might be responsible for the infrequent parasitism of longspurs.

One grassland host that appears to incur relatively high frequencies of parasitism is the Western Meadowlark. Despite reports from other regions that Western Meadowlarks recognize and reject cowbird eggs experimentally added to their nest (Peer et al. 2000), meadowlarks frequently were parasitized in this study (Table 4). In addition, high parasitism rates also have been reported in Manitoba (43%; Davis and Sealy 2000), Montana (30%; S. L. Jones unpubl. data), and North Dakota (47%; Koford et al. 2000). Other studies suggest that parasitism frequencies of grassland hosts vary geographically in the Great Plains (Koford et al. 2000). Maher (1973), for example, reported no parasitism of 15 meadowlark nests in Saskatchewan, and only 7% of Western Meadowlark nests were parasitized in Kansas (Hill 1976) and North Dakota (T. Grant and E. Madden unpubl. data).

Multiple parasitism was observed frequent-

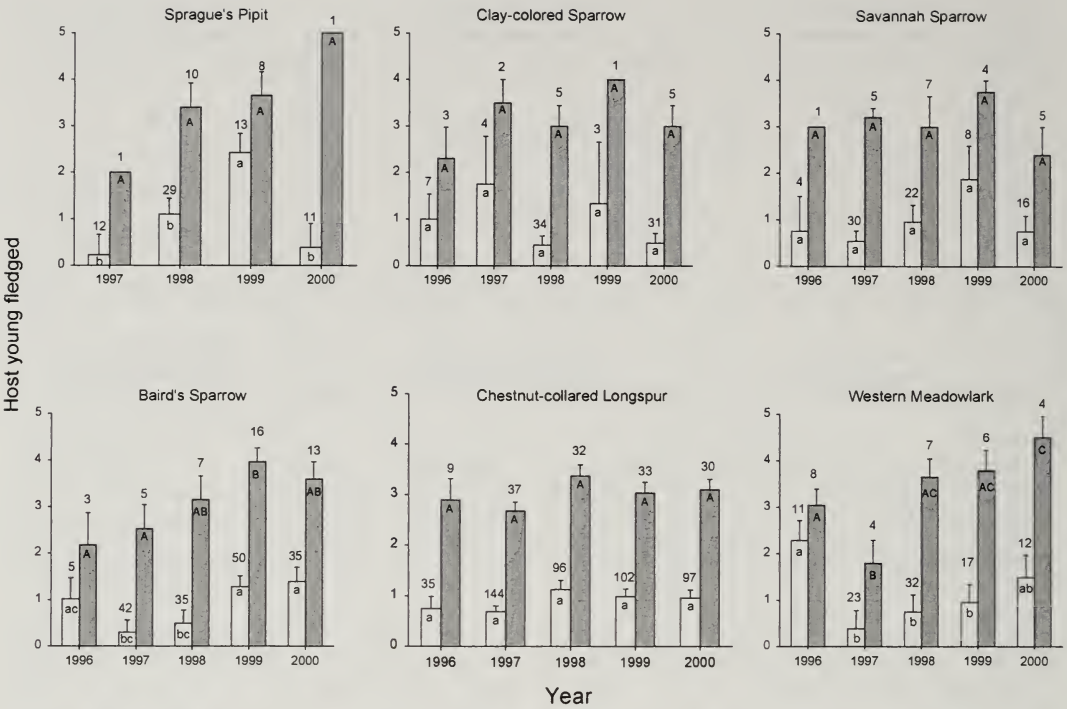

FIG. 4. Annual variation in mean (+SE) productivity for six grassland songbirds in southern Saskatchewan, 1996–2000. Sample sizes are above each bar for all nesting attempts (white bars) and successful nesting attempts (gray bars). Years sharing the same letter do not differ significantly ($P > 0.05$, one-way ANOVA) from each other.

ly in this study, as most parasitized nests contained as many as three cowbird eggs, except Clay-colored Sparrow and Western Meadowlark nests, which contained as many as two and four cowbird eggs, respectively. Western Meadowlark and Baird's Sparrow nests contained more cowbird eggs than any other grassland host in this study (Table 4). Davis and Sealy (2000) found that multiple parasitism was common in grassland hosts, as cowbirds laid 2.0–3.6 eggs per parasitized nest, and Western Meadowlarks received as many as eight cowbird eggs. Of the focal grassland birds in this study, Friedmann and Kiff (1985) listed only Savannah Sparrows, Clay-colored Sparrows, and Chestnut-collared Longspurs as hosts that are known to have reared cowbird young. However, both Western Meadowlarks

TABLE 4. Frequency and intensity of cowbird parasitism and cowbird productivity in nests of six common grassland hosts in southern Saskatchewan, 1996–2000. Sample sizes are in parentheses.

Species	Nests parasitized (%)	Parasitized nests with >1 cowbird egg (%)	Mean (± SE) number of cowbird eggs laid	Percentage of cowbirds fledged (cowbird eggs)	Mean (± SE) number of cowbirds fledged/nest	Mean (± SE) number of cowbirds fledged/ successful[a] nest
Sprague's Pipit	15.4 (65)	50.0 (10)	1.6 ± 0.22	0.0 (16)	0	0
Clay-colored Sparrow	26.8 (82)	27.3 (22)	1.3 ± 0.10	17.8 (22)	0.23 ± 0.11	1.00 ± 0.32 (5)
Savannah Sparrow	28.9 (83)	41.7 (24)	1.5 ± 0.15	11.1 (23)	0.17 ± 0.10	1.00 ± 0.00 (2)
Baird's Sparrow	20.9 (182)	60.5 (38)	1.7 ± 0.10	11.7 (36)	0.19 ± 0.09	0.70 ± 0.30 (10)
Chestnut-collared Longspur	16.3 (490)	27.5 (80)	1.3 ± 0.06	12.4 (76)	0.16 ± 0.05	0.40 ± 0.13 (20)
Western Meadowlark	25.2 (103)	61.5 (26)	1.8 ± 0.16	18.6 (24)	0.32 ± 0.13	0.70 ± 0.26 (10)

[a] Fledged at least one host or cowbird young.

TABLE 5. Clutch size, hatching success and productivity ($\bar{x}$ ± SE) were lower in nests that were parasitized than in nests that were not. Sample sizes are in parentheses. Data are from southern Saskatchewan, 1997–2000.

Species	Clutch size		Host eggs hatched		Host eggs incubated full term that hatched		Host young fledged/nest		Host young fledged/ successful nest[a]	
	Parasitized	Not	Parasitized	Not	Parasitized	Not	Parasitized	Not	Parasitized	Not
Sprague's Pipit	2.9 ± 0.60 (10)***	4.8 ± 0.12 (52)	0.2 ± 0.20 (9)***	2.7 ± 0.30 (53)	1.0 ± 1.00 (2)	3.2 ± 0.30 (45)	0.2 ± 0.20 (10)**	1.2 ± 0.25 (55)	2.0 ± 0.0 (1)	3.5 ± 0.32 (19)
Clay-colored Sparrow	2.4 ± 0.28 (20)***	3.8 ± 0.06 (57)	0.9 ± 0.26 (19)***	2.3 ± 0.23 (58)	1.4 ± 0.34 (12)*	2.6 ± 0.22 (51)	0.4 ± 0.19 (22)	0.6 ± 0.18 (56)	2.0 ± 0.32 (5)***	3.5 ± 0.22 (10)
Savannah Sparrow	2.9 ± 0.27 (21)***	4.4 ± 0.10 (53)	1.2 ± 0.31 (20)***	2.8 ± 0.26 (54)	1.8 ± 0.35 (14)***	3.3 ± 0.24 (44)	0.1 ± 0.09 (23)***	1.1 ± 0.22 (56)	1.0 ± 0.58 (3)**	3.2 ± 0.27 (19)
Baird's Sparrow	2.9 ± 0.19 (36)***	4.6 ± 0.05 (134)	1.5 ± 0.25 (34)***	2.7 ± 0.18 (128)	1.9 ± 0.26 (28)***	3.5 ± 0.17 (97)	0.6 ± 0.18 (37)	1.0 ± 0.15 (133)	2.1 ± 0.35 (10)***	3.9 ± 0.18 (34)
C-collared Longspur	3.2 ± 0.12 (78)***	4.2 ± 0.04 (381)	1.8 ± 0.17 (72)***	2.4 ± 0.10 (378)	2.3 ± 0.17 (54)***	3.2 ± 0.09 (287)	0.6 ± 0.13 (74)*	1.0 ± 0.08 (399)	1.9 ± 0.24 (24)***	3.2 ± 0.11 (119)
Western Meadowlark	4.0 ± 0.24 (25)***	5.1 ± 0.10 (66)	2.4 ± 0.38 (21)	2.6 ± 0.27 (73)	2.8 ± 0.36 (18)	3.4 ± 0.28 (56)	1.1 ± 0.31 (24)	1.0 ± 0.21 (71)	2.4 ± 0.41 (11)*	3.7 ± 0.26 (19)

[a] Nests fledging host or cowbird young.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

and Baird's Sparrows fledged cowbirds in this study (see also Davis and Sealy 1998, 2000). Sprague's Pipits failed to fledge cowbird young (Table 4), suggesting they are a poor quality host. Similarly, while Davis and Sealy (2000) found that pipits were capable of rearing cowbird young to fledging age in Manitoba, they recorded only one cowbird young fledging from nine eggs laid in pipit nests. Western Meadowlarks and Clay-colored Sparrows were especially productive hosts for cowbirds as they fledged the most cowbird young per parasitized nest.

Brown-headed Cowbirds typically lower the productivity of their hosts through egg removal or damage, and through competition with host nestlings (Payne 1977). Indeed, parasitized grassland hosts in this study experienced lower productivity due to a combination of reduced clutch size, hatching, and fledging success (Table 5). Davis and Sealy (2000) found that host egg removal was primarily responsible for the lower productivity in parasitized Baird's Sparrow nests in Manitoba. Although egg removal by cowbirds contributed to lower productivity of grassland hosts in the current study, as evidenced by the significantly smaller clutches in parasitized nests, all hosts also hatched fewer eggs in parasitized nests (Table 5). Cowbirds may have lowered hatching success of smaller hosts by incidentally damaging host eggs during the laying of their own eggs or when removing host eggs. Alternatively, cowbirds may have deliberately damaged or depredated host eggs during nest visits (Granfors et al. 2001). Overall, cowbirds cost grassland hosts between 1.3 and 2.2 young per successful nest (Table 5), similar to costs reported for hosts in Manitoba (Davis and Sealy 2000).

Conclusions.—The limited amount of demographic data on grassland birds in the northern Great Plains limits our ability to understand the life history of these species and to gain insight into causes of their population declines. Although nest predation was the most important factor associated with reproductive success of grassland songbirds in Saskatchewan, other factors, such as cowbird parasitism, may be equally or more important in other regions (Davis and Sealy 2000, Koford et al. 2000). Without additional information on aspects of their breeding ecology (e.g., pro-

pensity for renesting and raising multiple broods within a season) and other important demographic parameters (e.g., juvenile and adult survival), our understanding of the impact of nest predation and brood parasitism is incomplete. Also, this lack of information hinders our ability to identify population sources and sinks (Pulliam 1988) and to develop effective conservation measures for grassland birds. More studies are required to determine critical factors that influence the demography of grassland songbirds throughout the northern Great Plains.

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SURVIVAL AND REPRODUCTION OF WILD TURKEY HENS IN CENTRAL ONTARIO

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ABSTRACT.—Recent success of Eastern Wild Turkey (*Meleagris gallopavo silvestris*) reintroductions across southern Ontario has prompted wildlife managers to investigate the potential of extending the northern limit of this subspecies' range. We monitored the survival and reproduction of introduced Wild Turkeys on the Precambrian Shield in central Ontario during 1999–2001. Mean annual survival of 39 radio-tagged hens was 0.288 ± 0.057 SE. Summer and winter survival rates differed between the first and second years of the study. Spring and fall survival rates did not differ significantly between years. Reproductive parameters that characterized the population included a nesting rate of 0.588, mean clutch size of 10.0 eggs/nest, nest success of 0.500, hatching rate of 0.81, hen natality rate of 1.18 females hatched/female, poult survival of 0.54, and fall recruitment of 0.63 juvenile females/breeding hen. Success of the pilot Wild Turkey introduction in central Ontario was compromised by high predation, low numbers of introduced birds, and a prolonged period of deep snow during 2000–2001. *Received 14 November 2002, accepted 10 March 2003.*

The Eastern Wild Turkey (*Meleagris gallopavo silvestris*) was native to southwestern Ontario (Wintemberg 1919), but disappeared by 1907 due to unregulated hunting and habitat loss (Alison 1976). Reintroduction from various state Dept. of Natural Resources was initiated in 1984 (Weaver 1989), resulting in about 30,000 birds in the southern part of the province by 2000 (Bellamy 2001). The success of recent reintroduction efforts in southern Ontario, potentially favorable habitat alterations in central Ontario during the past century, and recent moderate winters prompted wildlife managers to consider pilot Wild Turkey introductions into presumably marginal northern habitats. Although the promiscuous breeding and high reproductive rate of Wild Turkeys (i.e., early breeders with large clutches) promote the species' likelihood to be successfully translocated (Griffith et al. 1989), small populations at the fringe of their geographic range incur a greater risk of extinction if either (1) predation rates are high, (2) Wild Turkeys are exposed to severe weather for prolonged periods of time, (3) food shortages force Wild Turkeys into unfavorable ranges, (4) number of other prey species is low, (5) current Wild Turkey populations are low, or (6) nesting cover is poor (Miller and Leopold 1992).

Wild Turkey populations are dynamic, which limits our understanding of the demographic parameters responsible for successful introduction into suboptimal habitats (Little and Varland 1981, Clark 1985, Miller et al. 1985, Weaver 1989). One potential factor responsible for changes in abundance at northern latitudes is winter mortality, where survival varies from 40% during severe conditions in forested landscapes to 93% during mild conditions in mixed agricultural and forested environments (Austin and DeGraff 1975, Wunz and Hayden 1975, Porter et al. 1980, Vander Haegen et al. 1988, Roberts et al. 1995). However, severe winters are sporadic, and associated mortality typically is a minor limitation on Wild Turkey abundance (Roberts et al. 1995). Nest success and poult survival are other factors limiting annual population change through reproduction (Vangilder et al. 1987, Roberts et al. 1995). Nest success typically varies between 31 and 62% (Porter et al. 1983, Vangilder et al. 1987, Vander Haegen et al. 1988, Roberts et al. 1995), and poult mortality within 2 weeks after hatching often varies between 60 and 92% (Little and Varland 1981, Speake et al. 1985, Vangilder et al. 1987, Vander Haegen et al. 1988).

There exists little, if any, survival and reproduction information on female Wild Turkeys inhabiting the Precambrian Shield, north

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of the species' historic range in central Ontario. It may be inappropriate to apply management strategies from published accounts of more southern Wild Turkey populations due to their annual fluctuations. Our objectives were to estimate survival and reproduction rates of newly introduced Eastern Wild Turkey hens in central Ontario, and to determine the relative importance of demographic parameters to annual population change. We hypothesized that (1) predator-induced mortality was greatest during nesting and brood rearing, and that (2) winter mortality in mixed agricultural and forested landscapes was not a limiting factor to annual population growth.

METHODS

Study area.—We conducted this study near Noëlville, located 60 km southeast of Sudbury (46° 10′ N, 80° 25′ W), Ontario, Canada. The 169-km^2 study area, delineated from movements of female radio-tagged Wild Turkeys, was located in the Great Lakes-St. Lawrence Ecotonal Forest Region (Rowe 1972), and characterized by flat to rolling topography (mean elevation of 210 m), interrupted by rock outcrops and narrow valleys. The landscape contains a mosaic of habitat, comprising approximately 20% coniferous forests, 37% deciduous forests, 16% agricultural land, 12% grass and meadow, and 15% residential areas and rock outcrops in parts of Bigwood, Cosby, Martland, Mason, and Scollard townships. Beef farming is the dominant industry, with most fields cultivated for corn silage or pasture grasses.

Fire, logging, and smelter emissions from Sudbury's mining operations destroyed or reduced much of the original climax vegetation, which included balsam fir (*Abies balsamea*), eastern white and red pine (*Pinus strobus*, *P. resinosa*), red oak (*Quercus rubra*), white spruce (*Picea glauca*), red and sugar maple (*Acer rubrum*, *A. saccharum*), and eastern hemlock (*Tsuga canadensis*; Rowe 1972). The resulting forests are dominated by white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*), with raspberry (*Rubus* spp.), bracken fern (*Pteridium aquilinum*), blueberry (*Vaccinium* spp.), beaked hazel (*Corylus cornuta*), and aster (*Aster* spp.) in the understory.

We obtained meteorological data (21 March 1999 to 20 March 2001) from Environment Canada, Sudbury. January was the coldest month of the year (mean temperature was −12.2° C), whereas July was the warmest month (mean temperature was 18.9° C). Mean annual rainfall was 73.9 cm from 21 March 1999 to 20 March 2000 and 51.1 cm from 21 March 2000 to 20 March 2001. Snowfall was 216.0 cm from November 1999 to March 2000 and 328.3 cm from November 2000 to March 2001, with snow depths exceeding 25 cm for 38 days from November 1999 to March 2000 and 111 days from November 2000 to March 2001.

Wild Turkey capture.—We captured 36 Eastern Wild Turkeys (10 males and 26 females), in southern Ontario and upper New York State, which were introduced during February and March 1999. Thirteen more hens from New York State were released in March 2000. All birds were captured with rocket nets (Hawkins et al. 1968), sexed, aged (Pelham and Dickson 1992), marked with patagial wing tags, and transported to the study area. We radio-tagged females with a backpack style 32.5-g mortality-mode VHF radio transmitter (Holohil Systems Ltd., Carp, Ontario). Transmitters represented about 1% of turkey body mass and were attached with 3.2-mm shock cord (Norman et al. 1997). The expected battery life was 150 weeks. We excluded from analyses birds that died within 14 days of release to reduce bias associated with capture-related stress and transmitter harness complications (Nenno and Healy 1979).

Survival.—We monitored instrumented female Wild Turkeys 5 days/week between 1 May and 31 August and 2–3 days/week between 1 September and 30 April and from 21 March 1999 to 20 March 2001. We obtained telemetry locations by triangulation from ≥3 locations (Heezen and Tester 1967) taken <15 min apart, with a 2-element H antenna and portable receiver-scanner (Model STR-1000, Lotek Engineering Inc., Newmarket, Ontario). We calculated seasonal survival rates for four time intervals: calendar spring, summer, fall, and winter. We recovered transmitters on mortality mode within 1–2 days to determine cause of mortality by examining the carcass and area surrounding the recovery site. When date of death was unknown, we assumed

death to have occurred midway between the previous and current monitoring dates.

We used the staggered entry design of the Kaplan-Meier method to determine survival rates ($\hat{S}$) and distributions (Pollock et al. 1989). We selected this method because newly instrumented Wild Turkeys were introduced into our study area during four separate releases, and it allowed for birds to be censored due to emigration or radio loss. We readmitted female Wild Turkeys that survived the year into the following year's data set (Roberts et al. 1995). We also estimated crude annual and seasonal survival rates, with predation as the only source of mortality, using the Kaplan-Meier approach by censoring all deaths not resulting from this agent (Kurzejeski et al. 1987). Mortality rates are not independent, and other mortality agents can influence this estimate (Heisey and Fuller 1985). Calculation of survival standard errors followed the method of Cox and Oakes (in Pollock et al. 1989). We used the log-rank test to determine annual differences in survival distribution. We used the *Z*-test statistic to examine differences in annual and seasonal survival rates.

Reproduction.—We determined nest locations by close range radio telemetry and triangulation. We flagged vegetation about 15 m around each nest site to prevent intrusions and nest abandonment by females. When telemetry indicated nest abandonment due to fledging, depredation, or other disturbances, we located the nest at the center of the flagged area. We excluded birds from the data set if research activities disrupted nesting (i.e., if hens did not return to their nests), except for information obtained prior to the disruption, such as nest site characteristics and clutch size. We defined nesting rate as the proportion of radio-tagged females that nested by 1 May, and renesting rate as the proportion of females that renested after an unsuccessful first attempt. The first date of incubation (five or more days of localized movements or inactivity) was used to determine nest initiation date and hatching date by subtracting 10 days for egg laying and adding 28 days for incubation (Healy 1992).

We defined nests as successful if one or more eggs hatched. We estimated clutch size by examination of eggshells and unhatched eggs. Because nest predators may remove some eggs, we considered this estimate as the minimum clutch size (Thogmartin and Johnson 1999). We determined the type of nest predation from predator tracks and eggshell breakage patterns (Cooper and Ginnett 2000). We assumed that the number of hatched eggs was equal to the initial brood size, and we defined hatching rate as the proportion of eggs that hatched in each clutch. Hen success was the probability that a nesting hen hatched one or more egg, regardless of the number of nesting attempts (Vangilder 1992). We calculated age specific female natality rates (m_x) as:

$$m_x = [(nr_x)(c_x)(ns_x)(hr_x)]/2,$$

where nr_x = nesting rate of age x, c_x = clutch size, ns_x = nesting success, and hr_x = hatching rate (Porter et al. 1983). We based clutch size and hatching rate during the first year of our study on one case due to difficulties in locating nests. We used flush counts to estimate poult survival (p_x), measured as the number of poults alive on 1 October, relative to the number hatched by all successful females. Despite the potential for brood adoption by co-occurring adult females, we assumed poults shared the same fate as maternal females that died before a flush count was conducted. We based first year poult survival on the number of poults alive in early fall relative to the number observed 14–28 days after hatching. We estimated recruitment of young females (R) into the fall population as the number of female poults/successful maternal female surviving to early fall (Porter et al. 1983):

$$R = (m_x)(p_x).$$

We used the log-likelihood ratio (Sokal and Rohlf 1995), median test (Sokal and Rohlf 1995), and Mann Whitney *U*-test to examine differences in reproductive parameters based on age and study year. The small 1999 sample size precluded comparison of clutch size between study years. We conducted statistical analyses with SPSS software (SPSS Institute, Inc. 1998).

RESULTS

Female survival rates.—Twenty-five of 26 and 12 of 13 radio-tagged Wild Turkey hens survived the 14-day adjustment periods during 1999–2000 and 2000–2001, respectively. We

censored 15 hens due to signal loss because of transmitter failure or bird emigration from the study area. Mean annual survival probability was 0.529 during 1999–2000 and 0.067 during 2000–2001, for a mean of 0.288 during the two years (Table 1). Annual survival distributions ($\chi^2 = 6.78$, df = 1, $P = 0.009$) and survival rates ($Z = 4.22$, $P < 0.0001$) differed significantly between years. Spring and fall survival rates were similar between years ($Z = 1.03$, $P = 0.30$ and $Z = 0.66$, $P = 0.51$, respectively). Female survival rates during summer and winter were greater ($Z = 1.86$, $P = 0.063$ and $Z = 3.26$, $P = 0.001$) during 1999–2000 (0.701 ± 0.121 SE and 0.900 ± 0.069 SE, respectively) than during 2000–2001 (0.381 ± 0.122 SE and 0.222 ± 0.196 SE, respectively).

Annual survival rate, with predation as the only source of mortality, was significantly greater ($Z = 2.30$, $P = 0.021$) during 1999–2000 (0.631 ± 0.093 SE) than during 2000–2001 (0.187 ± 0.169 SE; Table 2). Thirteen of 22 females were killed by mammalian predators, which included red fox (*Vulpes vulpes*), coyote (*Canis latrans*), dog (*Canis familiaris*), and fisher (*Martes pennanti*). Avian predators, as judged from decapitation, killed three hens. Seasonal survival rates due to predation were similar between years ($Z = 0.00$–1.34, $P = 0.18$–1.00). Predator-related deaths occurred primarily during summer ($n = 8$), followed by spring ($n = 4$) and winter ($n = 4$). Remaining deaths were attributed to poaching ($n = 1$), starvation ($n = 1$), hay mowing ($n = 1$), and unknown causes ($n = 3$).

Reproductive effort.—Median date for first nest initiation in 1999 (3 June) was not statistically different than that in 2000 (17 May; $\chi^2 = 0.11$, df = 1, $P = 0.73$). These dates varied between 1999 (7 May to 10 June) and 2000 (1 May to 25 June). Median date for renest initiation during 2000 was 13 June (range: 22 May to 28 June). Median first nest initiation dates did not vary significantly ($\chi^2 = 0.02$, df = 1, $P = 0.88$) between nests of adult (18 May, range: 1 May to 25 June) and juvenile hens (21 May, range: 7 May to 15 June). Mean clutch size did not vary significantly with female age ($U = 6$, $P = 0.77$, power = 0.05; Table 3). We found seven clutches of ≤4 eggs, and excluded them from clutch size

TABLE 1. Annual and seasonal Kaplan-Meier survival rates ($\hat{S}$), with 95% confidence interval, for radio-tagged Eastern Wild Turkeys in central Ontario, 21 March 1999 to 20 March 2001. Annual survival distributions ($\chi^2 = 6.78$, df = 1, $P = 0.009$) and survival rates ($Z = 4.22$, $P < 0.0001$) differed between years. Summer ($Z = 1.86$, $P = 0.063$) and winter ($Z = 3.26$, $P = 0.001$) survival rates were greater during 1999–2000 than during 2000–2001. Spring ($Z = 1.03$, $P = 0.30$) and fall ($Z = 0.66$, $P = 0.51$) survival rates were similar between years.

	1999–2000				2000–2001				Pooled			
Period[a]	$\hat{S}$	95% CI	SE	Risk[b]	$\hat{S}$	95% CI	SE	Risk	$\hat{S}$	95% CI	SE	Risk	Z-score
Annual	0.529	0.356–0.702	0.088	17	0.067	0.000–0.195	0.065	1	0.288	0.176–0.400	0.057	18	4.22
Seasonal													
Spring	0.923	0.784–1.00	0.071	13	0.789	0.575–1.000	0.109	11	0.854	0.723–0.985	0.067	24	1.03
Summer	0.701	0.464–0.938	0.121	10	0.381	0.142–0.620	0.122	6	0.545	0.364–0.726	0.092	16	1.86
Fall	0.909	0.640–1.000	0.137	4	1.000	1.000–1.000	0.000	5	0.933	0.774–1.000	0.081	9	0.66
Winter	0.900	0.765–1.000	0.069	17	0.222	0.000–0.607	0.196	1	0.678	0.500–0.857	0.091	18	3.26

[a] Annual (21 March to 20 March), spring (21 March to 20 June), summer (21 June to 21 September), fall (22 September to 20 December), and winter (21 December to 20 March).
[b] Maximum number of female turkeys at risk of dying during the period.

TABLE 2. Crude annual and seasonal survival rates ($\hat{S}$), with predation as the only mortality source, of radio-tagged Eastern Wild Turkeys in Noëlville, Ontario, 21 March 1999 to 20 March 2001. Annual survival rate was greater during 1999–2000 than during 2000–2001 ($Z = 2.30$, $P = 0.021$). Seasonal survival rates did not differ significantly between years ($Z = 0.000–1.34$, $P = 0.18–1.00$).

	1999–2000				2000–2001				Pooled			
Period[a]	$\hat{S}$	95% CI	SE	Risk[b]	$\hat{S}$	95% CI	SE	Risk	$\hat{S}$	95% CI	SE	Risk	*Z*-score
Annual	0.631	0.449–0.813	0.093	17	0.187	0.000–0.519	0.169	1	0.416	0.269–0.563	0.075	18	2.30
Seasonal													
Spring	0.923	0.784–1.000	0.071	13	0.789	0.575–1.000	0.109	11	0.854	0.723–0.985	0.067	24	1.03
Summer	0.761	0.529–0.993	0.118	10	0.534	0.242–0.826	0.149	6	0.656	0.187–1.000	0.239	16	1.19
Fall	1.000	1.000–1.000	0.000	4	1.000	1.000–1.000	0.000	5	1.000	1.000–1.000	0.000	9	0.00
Winter	0.900	0.765–1.000	0.069	17	0.445	0.000–1.000	0.332	1	0.745	0.570–0.920	0.089	18	1.34

[a] Annual (21 March to 20 March), spring (21 March to 20 June), summer (21 June to 21 September), fall (22 September to 20 December), and winter (21 December to 20 March).
[b] Maximum number of female turkeys at risk of dying during the period.

analysis because they apparently had been depredated. Raccoons (*Procyon lotor*) presumably disturbed two of these clutches, based on tracks found near the nest. One nest was depredated by a red fox, indicated by teeth marks on eggshells, one by a Common Raven (*Corvus corax*; LPN pers. obs.), and three by unknown predators. Hatching rates did not differ significantly ($U = 3$, $P = 0.64$, power = 0.05) between adult (0.81 ± 0.05 SE) and juvenile females (0.80 ± 0.10 SE).

Nesting rate of adult females was not significantly different ($G = 1.29$, df = 1, $P = 0.26$, power = 0.59) than that of juvenile birds (0.682 and 0.417, respectively). Nesting rates also were not significantly different ($G = 1.79$, df = 1, $P = 0.18$, power = 0.05) between 1999 and 2000 (0.438 and 0.722, respectively). No differences in nest success were evident between age classes or years (all G values < 0.01, df = 1, $P = 1.00$). Natality rate in 1999 was 1.0 female hatched/female in the breeding population, whereas 1.3 females hatched/female in 2000. Adult hen natality was 1.3 females hatched/female in the breeding population, and 0.4 females hatched/female for juvenile hens. Poult survival of adult birds was 0.68, and 0.17 for juvenile hens. Fall recruitment was 0.63 juvenile females/breeding hen.

DISCUSSION

Our mean annual survival rate of hens was less than in populations introduced to Indiana (Miller et al. 1985), Iowa (Little and Varland 1981), and Ohio (Clark 1985). Different methodologies used to calculate survival rates and standard errors may, in part, explain our low survival rates. Disadvantages of their method to calculate mortality rates by dividing number of radio-tagged hens dead per month by the number alive at the beginning of the month are that survival is biased if censored observations are excluded from analysis, and that survival is assumed constant throughout each month (Kurzejeski et al. 1987). The Kaplan-Meier procedure does not have these disadvantages (Pollock et al. 1989). Annual survival during 1999–2000 was similar to those of established populations in northern Missouri (Kurzejeski et al. 1987) and southcentral New York (Roberts et al. 1995). Survival during 2000–2001 was the least reported for this

TABLE 3. Reproductive parameters of Eastern Wild Turkey hens in Noëville, Ontario, 1999–2000.

	Nesting rate (*n*)	Clutch size (*n*)	Nest success (*n*)	Hatching rate	Natality rate[a]	Poult survival[b]	Recruitment rate[c]
Year							
1999	0.438 (7)	9.0 (1)	0.571 (4)	0.89	1.00	0.68	0.68
2000	0.722 (13)	10.1 (8)	0.461 (6)	0.79	1.33	0.39	0.52
Age							
Adult	0.682 (15)	10.0 (7)	0.467 (7)	0.81	1.29	0.68	0.88
Juvenile	0.417 (5)	10.0 (2)	0.250 (3)	0.80	0.42	0.17	0.07
Total	0.588 (20)	10.0 (9)	0.500 (10)	0.81	1.18	0.54	0.63

[a] Number of females hatched/female in the breeding population.
[b] Proportion of poults surviving through summer.
[c] Number of young females recruited into the fall population per successful nesting hen.

subspecies, which was attributed to high summer and winter mortality (Table 1). We realize that small sample size may limit our conclusions to this study because findings may not accurately reflect actual population parameters.

We did not evaluate if hen survival was a function of nesting-related activities, but incidental observations suggest this possibility. High hen mortality during this period may be attributed to several factors, but are not limited to (1) an increase in predator populations (Weaver 1989), (2) exposure to abnormal weather conditions for prolonged periods of time (Vangilder et al. 1987, Roberts et al. 1995), (3) poor nesting cover (Bowman and Harris 1980, Clark 1985), (4) a behavioral response of hens to low body mass by foraging more frequently (Porter et al. 1983, Thogmartin and Johnson 1999), and (5) low availability of other prey species (Miller and Leopold 1992). Predation accounted for 58% of hen turkey mortality, with losses during summer being the greatest (Table 2). Our data indicated differences between years for annual predator-related mortality rates, but we could not link this observation to high predator populations or low prey abundance. Roberts et al. (1995) hypothesized that warm, wet weather during spring and summer may facilitate nest location by predators by enhancing olfactory cues. Although we observed greater hen mortality after prolonged periods of rain during the 2000 breeding period, we found no evidence to suggest that hen mortality was related to rainfall ($r_s = -0.20$, $P = 0.47$, power = 0.004). High mortality occurred during 1999 when mean precipitation was above the 30 year normal, whereas low mortality occurred the following year when mean precipitation was below normal (Nguyen 2001). Dry weather may affect spring phenology by reducing vertical nest cover to increase predator search efficiency (Bowman and Harris 1980, Rolley et al. 1998).

Fluctuations in winter survival between 1999–2000 (0.900) and 2000–2001 (0.222) likely were due to variation in winter severity (Austin and DeGraff 1975, Wunz and Hayden 1975, Porter et al. 1980, Vander Haegen et al. 1988). High survival during 1999–2000, characterized by favorable snow conditions and abundant food supply, was consistent with rates observed during mild winters in Massachusetts (0.930; Vander Haegen et al. 1988), Minnesota (0.850; Porter et al. 1983), and New York (0.873; Roberts et al. 1995). Severe winter conditions have been associated with reduced survival of turkey populations at northern latitudes: 0.450 in Minnesota (Porter et al. 1983), 0.370 in New York (Austin and DeGraff 1975), and 0.600 in Pennsylvania (Wunz and Hayden 1975). We found no differences in predator-related winter mortality between 1999–2000 and 2000–2001, probably due to our small sample of hens at risk during 2000–2001. Predation and starvation probably were the major sources of winter mortality during this period; however, we did not have information to test these hypotheses.

Although we detected no statistical difference in median nest initiation date between 1999 (3 June) and 2000 (17 May), this difference of two weeks may be biologically significant. Introduced hens surviving their first year may be familiar with local habitats, and

thus reduce the time needed to locate suitable nest sites, as compared to inexperienced, newly introduced birds. Alternatively, capture-related stress may reduce energy reserves of newly introduced birds. The nutritional condition of hens may, in part, explain delays in nest initiation, foregoing of nesting, and clutch size (Thogmartin and Johnson 1999). Porter et al. (1983) suggested that a threshold body mass may exist; consequently, hens may delay nesting until nutrient reserves can be replenished.

Nest success in our study was greater than those reported in Arkansas (Thogmartin and Johnson 1999), Missouri (Vangilder et al. 1987) and New York (Roberts et al. 1995), but less than that reported in Minnesota (Porter et al. 1983). Mean nest success was similar to those reported in Virginia and West Virginia (Norman et al. 2001) and Massachusetts (Vander Haegen et al. 1988). Clutch size of 10.0 eggs found in our study was identical to those reported in northern Missouri (Vangilder et al. 1987), greater than the 8.8 eggs found in Arkansas (Thogmartin and Johnson 1999), but less than the 11.6 eggs reported in Iowa (Little and Varland 1981), 12.1 eggs in Massachusetts (Vander Haegen et al. 1988), 11.8 eggs in Minnesota (Porter et al. 1983), 12.0 eggs in New York (Roberts et al. 1995), 12.0 eggs in Ohio (Clark 1985), and 11.9 eggs in southern Ontario (Weaver 1989).

Natality rate in this study was less than those reported for adult and juvenile hens in Minnesota (Porter et al. 1983) and Massachusetts (Vander Haegen et al. 1988). Lower natality rates for adult and juvenile hens were reported for a population in decline in Arkansas (Thogmartin and Johnson 1999). The recruitment rate found in this study was similar to that reported in Massachusetts (Vander Haegen et al. 1988), but less than that reported in Minnesota (Porter et al. 1983). Failure to locate more than one nest in 1999 biased estimates of productivity, especially nesting rate and poult survival.

Our study indicates that a number of selective pressures (e.g., predation and weather) may have influenced Wild Turkey survival and reproduction. We cannot, however, discriminate among selection pressures without manipulation experiments. Although we suggested that predation and starvation may have been the major mortality factors in our study, they were not limiting factors. Many of the reproductive parameters we measured were comparable to those reported in southern Ontario (Weaver 1989), Minnesota (Porter et al. 1983), and Ohio (Clark 1985), where turkey populations have flourished. Currently, the population in our study area is estimated at 30–35 turkeys (K. Bellamy pers. comm.). This small population indicates that Wild Turkeys can survive and reproduce north of the species' historic range in Ontario.

Populations introduced in similar areas may not experience a rapid population growth as counterpart populations in southern Ontario (Weaver 1989, Bellamy 2001). In these areas, management for this species may require rigorous winter habitat improvement, such as planting shrubs that bear fruit late into the winter, to increase food availability above the snow. Since severe winters tend to occur approximately every fifth year in our region (Nguyen 2001), supplemental feeding may be necessary to maintain turkey numbers. However, this management strategy should be considered as a last resort because supplemental feeding can cause birds to aggregate, making them more susceptible to predation.

Wild Turkey introduction programs in similar areas (i.e., outside of their historic range) should take into consideration the habitat requirements of turkeys in the source population. For example, introducing birds to areas with different habitat structures may preclude those birds from recognizing the appropriate habitat features (Healy 1992, Badyaev 1995), which may lead to reduced survival and/or reproductive performance. In our study, we did not observe Wild Turkeys using manure piles for winter survival either because of unfamiliarity with potential food resources associated with manure and/or instinctive wariness of Wild Turkeys to approach areas with cattle. Introduction of birds to areas with different habitat structure is not well studied, and deserves further attention.

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SURVIVAL AND HABITAT OF RUFFED GROUSE NESTS IN NORTHERN MICHIGAN

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ABSTRACT.—Effective management of Ruffed Grouse (*Bonasa umbellus*) populations requires a full understanding of chick production. Previous reports of nest survival for Ruffed Grouse are biased because they did not account for successful nests being more likely to be found, and the role of habitat quality in determining nest survival is unknown. We determined survival rates of Ruffed Grouse nests in northern lower Michigan using the less biased Mayfield estimator, defined differences between first and second nests, and compared the local habitat characteristics of successful and unsuccessful nests. Median hatching dates were 10 June for first nests (n = 34) and 1 July for second nests (n = 6). First nests had a lower survival rate (0.442, 95% CI = 0.270–0.716), a higher mean clutch size (12.7 eggs ± 0.3 SE), and higher egg hatching rate (0.960, 95% CI = 0.900–0.997) than did second nests (nest survival = 0.788, 95% CI = 0.491–1.00; clutch size = 7.3 eggs ± 0.3 SE; and hatching rate = 0.826, 95% CI = 0.718–0.925). Nest survival, annual production (3.4 hatchling females/adult female, 95% CI = 2.3–5.0), and fall recruitment (1.0 juvenile females/adult female, 95% CI = 0.3–2.4) were less than previously reported estimates. Habitat characteristics at nest sites varied widely and did not differ appreciably between successful and unsuccessful nests. *Received 16 July 2002, accepted 22 February 2003.*

Although the importance of nest success to understanding grouse population fluctuations has been recognized (Gullion 1970), it remains little studied. Brander (1967), Barrett (1970), and Maxson (1974, 1978a) studied the behavior of female grouse during the breeding season, and information about hatching dates and clutch size has come from many sources (Hale and Wendt 1951, Cringan 1970, Rusch and Keith 1971, Porath and Vohs 1972, Kubisiak 1978, Maxson 1978b, Small et al. 1996). A full understanding of grouse chick production, however, is lacking because little information is available for nest survival rates, renesting attempts, and nesting habitat.

Survival rates of Ruffed Grouse (*Bonasa umbellus*) nests, some based on large samples (Bump et al. 1947), have been reported only as the percentage of observed nests that hatched chicks (Rusch and Keith 1971, Maxson 1978b, Small et al. 1996). This apparent survival rate contains substantial positive bias because successful nests are more likely to be located by researchers (Mayfield 1961, Johnson 1994). The degree of bias may not be constant among studies, so comparing apparent survival rates among different areas or time periods may not be appropriate. Accurate quantitative estimates of nest survival are necessary for comprehensive evaluation of population vital rates (i.e., survival and reproductive success rates) and demographic simulation modeling.

Annual fertility (i.e., hatchling females/adult female; Johnson 1994) is only partially dependent upon nest survival. An accurate estimate of fertility also depends upon clutch size and the rates at which females attempt multiple nests within a single breeding season (Caughley 1977). The second nesting attempt of a marked female grouse after failure of the first nest was first documented by Barrett (1970). The only additional data for known second nests were reported by Small et al. (1996). The assumption of renesting often is based on evidence of a secondary peak in hatching that usually involves notably smaller clutches (Cringan 1970, Porath and Vohs 1972, Maxson 1978b). The survival rate of second nests may be different from first nests because most second nests are at risk later in the spring, when environmental conditions such as weather and predation pressure may be different.

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The significance of habitat quality to chick production needs further study (Martin 1995). Bump et al. (1947), Gullion (1977), Maxson (1978b), and Thompson et al. (1987) have described nest sites, but few have related their findings to nest survival rates. Also, no one previously has quantified the amount of cover at nest sites. Our objectives were to determine nest survival rates, to define differences between first and second nests, and to compare the habitat characteristics of successful and unsuccessful nests.

METHODS

Study area.—We conducted our study in the northern portion of the lower peninsula of Michigan. Study sites were located in the Huron National Forest (HNF; 44° 32′ N, 83° 58′ W) and Pigeon River Country State Forest (PRCSF; 45° 11′ N, 84° 26′ W). Each covered approximately 200 km^2 and was selected because it was perceived to contain high quality Ruffed Grouse habitat. The HNF site was dominated by stands of aspen (*Populus* spp.), mixed hardwoods (e.g., *Acer* spp.), and oaks (*Quercus* spp.). The PRCSF site was approximately 100 km to the north of the HNF site and was similar but had fewer stands of oaks and more stands of conifers (*Pinus resinosa*, *P. strobus*, *Thuja occidentalis*). Detailed information about the forest structure, overstory vegetation, and Ruffed Grouse habitat at both sites is in Gormley (1996). A weather station 19 km northwest of the HNF site recorded the following conditions. April 1996: precipitation sum = 7.5 cm, mean daily low temperature = −3.2° C, mean daily high temperature = 8.6° C; May 1996: precipitation sum = 3.6 cm, mean daily low temperature = 2.5° C, mean daily high temperature = 17.0° C; April 1997: precipitation sum = 1.9 cm, mean daily low temperature = −2.4° C, mean daily high temperature = 11.4° C; and May 1997: precipitation sum = 5.9 cm, mean daily low temperature = 2.4° C, mean daily high temperature = 14.1° C (Midwestern Climate Center, Champaign, Illinois, unpubl. data).

Chick production.—We located nests during spring, 1996 and 1997, by monitoring female grouse that had been captured and marked with a radio transmitter the previous fall (see Clark 1996). We approached females if radio tracking indicated that they were in the same location on two consecutive days. Once nests were found, we monitored them every 1–5 days, considering them active if radio tracking indicated that the female was on the nest. We approached nests for visual inspection only to determine final clutch size and when the female was not at the nest. Within two days after a nesting attempt was complete, we counted the number of eggs that did, and did not, hatch, marking an attempt as successful if ≥1 egg hatched. We monitored unsuccessful females to locate renesting attempts and observed second nests using methods identical to those for first nests. All procedures for capturing, handling, and marking grouse were reviewed and approved by the Michigan State Univ. All-University Committee on Animal Use and Care (AUF# 10/93–400–03).

We estimated clutch initiation dates from the earliest known point in the nesting sequence. If we found a nest during the egg-laying period, we subtracted 1.3 days for each egg from the earliest date during which we observed an incomplete clutch (Maxson 1974). If we found a nest during incubation, the clutch initiation date could be determined only if the nest was successful. In this case we subtracted from the hatching date 1.3 days to lay each egg in the full clutch and a 25-day incubation period beginning with the last egg.

Habitat characteristics.—We obtained the age and dominant overstory vegetation type of forest stands containing marked grouse nests from the U.S. Forest Service and the PRCSF headquarters. After the nesting attempt was complete and the female was no longer occupying the nest, we analyzed characteristics of each nest site. We sampled nesting habitat at the HNF site on 11–15 June 1996 and 11 June to 3 July 1997. We sampled at the PRCSF site on 7 July 1996 and 7 August 1997. We noted the direction and distance between nests and any solid objects within 1 m. We recorded aspect of the ground slope as one of eight general compass directions. We counted live woody stems ≥1 m tall in a 10 × 10-m plot centered on the nest. We quantified cover at the nest site as estimates of percent visual obstruction of a 1-m-tall profile board from 5 m and 15 m in front of the nest, a 1 × 1-m ground cover plot centered on the nest, and a spherical densiometer view of can-

opy cover above the nest (Higgins et al. 1994). We also measured the distances from the nest to the nearest opening (no live woody stems and no canopy cover for 5 m in one straight line dimension), mature aspen tree (≥15 cm dbh), and conifer tree (≥1 m tall). A more detailed description of field methods is in Larson (1998).

Data analysis.—We used the Mayfield (1961) method to calculate nest survival rates and the methods of Johnson (1979) to calculate the SE of survival rates and of differences in survival among categories. When >1 day elapsed between the last two nest checks, we used the midpoint as the date of nest success or failure. To evaluate potential underestimation of variance in survival rates (Ford et al. 2001), we simulated and analyzed 10,000 bootstrap samples of our empirical data (Efron and Tibshirani 1993). We also simulated 10,000 bootstrap samples to construct confidence intervals (CIs) on egg hatching rates and used nests as the sampling unit rather than eggs. We estimated chick production and fall recruitment for the population by multiplying the CIs (Moore 1979) of clutch size, nest survival, egg hatching rate, and chick survival from a concurrent study (approximately 0.302 ± 0.091 SE; Larson et al. 2001).

Due to the descriptive nature of our study and relatively small sample sizes, we avoided statistical hypothesis testing and modeling (e.g., logistic regression) in favor of estimating the magnitude and precision of important differences. We searched for differences in chick production variables (e.g., clutch initiation date, clutch size, survival rate) and habitat characteristics of nest sites between levels of variables such as age of the female, nesting attempt, and nest fate. Most of our data were not normally distributed, so we based our calculation of estimated differences and CIs (exclusive of nest survival) on statistics associated with Wilcoxon's rank sum (Hollander and Wolfe 1973:75–79). We often present CIs or ranges rather than SD or SE because the latter do not represent the asymmetrical nature of uncertainty around many of our estimates.

RESULTS

Chick production.—We observed 41 nesting attempts by 34 female grouse. Six of the 35 first nesting attempts were made by three females observed both years, and four were made by females subsequently observed making a second nesting attempt during the same year. We observed two additional second nests made by females whose first nests we did not locate. Of the other 25 observed first nests, we excluded one from all survival analyses (but included it in the estimation of habitat characteristics) because it was found after it had been destroyed by a predator, one from all habitat analyses (including survival estimated by habitat categories) because we did not sample habitat at that nest site, and two others from estimation of habitat characteristics because they were abandoned when the female was killed away from the nest.

The date of clutch initiation ranged from 26 April to 4 June. The median date for first nests (n = 27) was 1 May. Nesting appeared to begin approximately four days earlier in 1997 than in 1996 (95% CI = 0–7 days). Of the five second-year (SY) females that survived the destruction of their first nest, only two made a second attempt at nesting. All four of the after-second-year (ASY) females in the same situation, however, made a second nesting attempt. Two females that attempted second nests had been incubating for 9 and 13 days, respectively, when their first nest was destroyed. The date of first nest destruction for females that subsequently attempted a second nest was as late as 28 May. Second clutches were initiated 3–6 days after the destruction of the first nest. The median date of second clutch initiation was 29 May (n = 6).

Nests hatched between 4 June and 3 July. The median was 10 June for first nests (n = 23) and 1 July for second nests (n = 5). Three first nests had known incubation times of 24, 25, and 27 days for clutches of 13, 13, and 14 eggs, respectively. Two second nests had known incubation times of 21 and 26 days for clutches of eight and seven eggs, respectively.

The mean full clutch size was 12.7 eggs ± 0.3 SE for 30 first nests and 7.3 eggs ± 0.3 SE for 6 second nests. Mean clutch size was smaller for SY females than for ASY females for first (a difference of 0.2 eggs ± 0.6 SE) and especially second nests (a difference of 1.3 eggs ± 0.5 SE). All eggs hatched in 83% of the 23 successful first nests and 20% of the 5 successful second nests. Mean hatching rates were 0.960 (95% CI = 0.900–0.997) and

TABLE 1. Characteristics of Ruffed Grouse nests observed in northern Michigan during 1996 and 1997.

Characteristic	*n*	Mean ± SE or median (5th–95th percentiles)
DSR[a]	40	0.9832 ± 0.0048
DSR during 1996	12	0.9814 ± 0.0092 (0.9809 ± 0.0091)[b]
DSR during 1997	28	0.9840 ± 0.0056 (0.9835 ± 0.0060)
DSR of first nests	34	0.9807 ± 0.0058 (0.9804 ± 0.0059)
DSR of second nests	6	0.9930 ± 0.0070 (0.9928 ± 0.0073)
DSR of SY females[c]	20	0.9797 ± 0.0076
DSR of ASY females[c]	19	0.9885 ± 0.0057
DSR during egg laying	11[d]	0.9524 ± 0.0465
DSR during incubation	36[d]	0.9895 ± 0.0040
Diameter of nest object (cm)[e]	34	10 (2–30)
Horizontal cover (%)[f] from 5 m	38	45 (10–85)
Horizontal cover (%)[f] from 15 m	38	85 (25–100)
Ground cover (%)[f]	38	53 (15–85)
Canopy cover (%)[f]	38	90 (59–99)
Distance to opening (m)[g]	38	14 (2–224)
Distance to aspen (m)[g]	38	12 (0–165)
Distance to conifer (m)[g]	38	2 (0–240)

[a] DSR = daily survival rate of nests.
[b] Estimates in parentheses are from 10,000 bootstrap samples.
[c] SY = second-year; ASY = after-second-year.
[d] Number of nests known to be in the nesting stage during ≥1 of the days it was under observation (i.e., some nests represented both stages). One nest failed during 21 days of observation of nests known to be in the egg laying stage, and seven nests failed during 663.5 days of observation of nests known to be in the incubation stage.
[e] Diameter of the tree, snag, stump, log, or branch against or under which the nest was built.
[f] Percent visual obstruction of a 1-m-tall profile board (horizontal cover), of bare ground from a 1.5-m height (ground cover), or above 1.5 m estimated using a spherical densiometer (canopy cover).
[g] Distance from the nest to the nearest opening with no live woody stems or canopy cover for ≥5 m in one straight-line dimension, live aspen tree ≥15 cm dbh, or live conifer tree ≥1 m tall.

0.826 (95% CI = 0.718–0.925) for successful first and second nests, respectively.

We observed nests for 714 nest-days (median = 20 days/nest). Twenty-eight nests were successful, 10 were destroyed by predators, and two were abandoned when the female was killed while away from the nest. The mean daily survival rate was 0.9832 ± 0.0048 for all nests. Our sample of first nests surviving to hatch were at risk a mean of 40.1 days, and second nests were at risk for 32.6 days. Using the same daily survival rates and standard nest durations of 42 and 34 days, however, survival rates for the entire nesting interval were 0.491 (95% CI = 0.327–0.733) for first nests and 0.562 (95% CI = 0.405–0.777) for second nests. Our data do not support differences in daily survival rates by nest stage, nesting attempt, year, age of female, or any categorical habitat characteristics of nest sites (Table 1). The SE of daily survival rate in bootstrap samples indicated almost no bias in our original estimates of precision (Table 1).

First nests produced a mean of 6.0 (95% CI = 3.8–9.3) hatchlings per female (nest survival × clutch size × egg hatch rate = 0.491 × 12.7 × 0.96). Second nests produced a mean of 3.4 (95% CI = 2.2–5.1) hatchlings per female (0.562 × 7.3 × 0.83). Only 6 of 13 females with a destroyed first nest, however, made a second nesting attempt, and they represented approximately 23% of the population of females that began the breeding season ([1 − 0.491] × 0.46). Therefore, a mean of 6.8 (95% CI = 4.5–10.0) hatchlings were produced per female present in the spring population (6.0 + [0.23 × 3.4]). Survival of those hatchlings was approximately 0.302 (Larson et al. 2001), so recruitment into the fall population was 2.1 (95% CI = 0.6–4.8) juveniles per spring female.

Habitat characteristics.—Overall, forest stands containing marked grouse nests were a median of 32 (5th–95th percentiles range = 13–81, n = 28) years old with a median of 6,050 (5th–95th percentiles = 2,000–24,400, n = 38) woody stems/ha. Equal numbers (13 each) of Ruffed Grouse nests were located in aspen and conifer overstory vegetation categories, but fewer nests were in other decidu-

ous types (n = 9). One nest was at the edge of a grassy opening and four were located on private property where overstory vegetation types were not defined. All females (n = 40) positioned their nests against one of five objects: a live tree (62.5%), a snag (12.5%), a log (12.5%), a branch laying on the ground (7.5%), or a stump (5.0%). Seven live nest trees were aspens, 10 were other deciduous species, and 8 were conifers. Second nests were positioned against larger objects (median = 25 cm in diameter, n = 5) than were first nests (median = 10 cm, n = 31; median difference = 15 cm, 95% CI = 5–23 cm). Nests were found in similar proportions on all sides of objects. Although 23 nests were located on level ground, 14 of 17 nests on slopes had at least some southern or eastern exposure. We found no other appreciable differences in nesting habitat between successful and destroyed nests, first and second nests, or the nests of SY and ASY females (i.e., the CI on differences included zero).

DISCUSSION

Chick production.—Ruffed Grouse clutch initiation and hatching dates are thought to be highly dependent upon latitude, with the nesting season beginning earlier in the more southern portions of its range (Maxson 1978b). Working in three areas of Michigan within 100 km of the HNF and PRCSF sites, Fisher (1939) reported a mean hatching date of 9 June, excluding one nest that hatched on 8 July. These dates and those reported by Maxson (1978b; 4–8 June) for a similar latitude in Minnesota closely matched the hatching dates of first and second nests we observed. Our estimates of hatching dates were approximately 1–2 weeks later than those found at lower latitudes (Bump et al. 1947: 284, Cringan 1970, Porath and Vohs 1972, Kubisiak 1978). Porath and Vohs (1972) reported a peak in the hatching of second nests three weeks after the peak for first nests in southern Ontario. The difference between the median hatching dates of first and second nests in our study was exactly 21 days, which suggests that the timing of second nests relative to first nests may be consistent regardless of latitude. The possible earlier nesting during 1997 may be attributable to the warmer, drier weather during the month of April that year.

It has been considered unlikely that female grouse would attempt a second nest if they had begun incubation of their first nest before it was destroyed by a predator (Bump et al. 1947:291). Two females in our study renested after incubating their first nest for 1–2 weeks, and five renesting hens in Wisconsin incubated first nests for 5–18 days (Small et al. 1996). Stage of the nesting sequence, therefore, may not be as important to the probability of renesting as previously thought (Bump et al. 1947:291). Although renesting may be more likely to occur for extremely early first nest failures (e.g., early May) than for extremely late failures (e.g., early to mid-June), we have presented evidence that the age of the female may affect the likelihood of renesting during mid- to late May.

Our estimate of first nest clutch size is greater than the means of 11.5 and 11.9 eggs in "early nests" found in other studies (Bump et al. 1947:361, Cringan 1970) and the means of 10.6–12.5 eggs reported by those who did not distinguish between first and second nests (Leopold 1933:362, Fisher 1939, Fallis and Hope 1950, Rusch and Keith 1971, Maxson 1978b). Our estimate of clutch size for second nests is less than the means of 7.5 and 8.5 eggs in "late nests" reported by Bump et al. (1947:361) and Cringan (1970), respectively. The differences between the results for clutch size from this study and others may be due to the lack of, or imprecise, classification of first and second nests during earlier studies. Clutch size for known first nests in Wisconsin (11.0), however, also was less than in our study, whereas clutch sizes of known second nests were similar (7.4 versus 7.3 in our study; Small et al. 1996).

In New York, Bump et al. (1947:365) observed that the rate of egg hatching in successful "late nests" was approximately 2% less than in "earlier nests." The same was observed by Small et al. (1996), but their rates were much lower (about 0.44). We found a larger decrease in the egg hatching rate in second nests (12.6%).

Bump et al. (1947:359–360) suggested that SY females may produce smaller clutches than ASY females. Their conclusion was based on captive grouse and one wild female with clutches of 10, 13, and 12 eggs when she was one, two, and five years old, respectively.

Maxson (1978b), however, reported no difference in clutch size between SY and ASY females. Our results agree with those of Bump et al. (1947:359–360) and Small et al. (1996), and suggest that perhaps the variability in clutch size among females prevents the detection of a difference in clutch size according to age that is apparent within individual females.

Estimates of apparent nest survival for Ruffed Grouse range from 0.46 to 0.86 (Bump et al. 1947:312, Rusch and Keith 1971, Maxson 1978b, Small et al. 1996). Because most nests are not located until after incubation begins, including those of radio-tagged females, one cannot account for the significant, but unknown, number of nests that are destroyed during the egg-laying period with the apparent survival method. Although our Mayfield nest survival estimate for second nests (0.79) falls within the range of apparent nest survival rates, our Mayfield survival estimate for first nests (0.44) is substantially below most previous estimates. Chick production, therefore, is likely less than previously reported. This has implications for the relative importance of reproduction and fall-to-spring survival in the fluctuations of Ruffed Grouse populations. Given that both nest and chick survival (Larson et al. 2001) may be less than previously expected, concern about recruitment of new individuals into the fall population may increase.

Habitat characteristics.—Our sample of Ruffed Grouse nests was too small for us to detect differences in habitat characteristics between successful and destroyed nests because of the high variability in the vegetation data. Nearly all dominant overstory vegetation types were used. Less than 5% of nests in studies by Bump et al. (1947:127–128) and Maxson (1978b) were located in conifer cover types, but more than a third of the nests in our study were located in conifer stands. The age of a forest stand also appears to be less important than the actual cover it provides. Gullion (1977) reported that aspen stands between 25 and 30 years old provide preferred nesting habitat because stem densities are <4,900 stems/ha and the closed canopy prevents the growth of dense understory vegetation, which supposedly aids the incubating female in detecting predators. By comparison, none of the 13 aspen stands that contained nests during our study were 25–30 years old; nine were younger, four older. The females in our study nested in forest stands of nearly all seral stages, which is consistent with the results of Bump et al. (1947:127–128).

Although stem density results from a study of Ruffed Grouse nest sites in an oak-hickory (*Carya* spp.) forest (Thompson et al. 1987) agree with Gullion's (1977) prediction of preferred nesting cover in areas with low stem densities, fewer than half of the nest sites in our study were in areas of <4,900 stems/ha. This probably is due to the definition of a stem that was used. Stem density measurements that include only relatively large stems (e.g., >2–3 cm dbh) are better descriptors of the quality of grouse nesting habitat because they indicate the degree of forest thinning to which Gullion (1977) was referring. On the other hand, using a less restrictive definition (e.g., woody stems >1 m tall), as we did following a definition by Cade and Sousa (1985), seems to provide a redundant measure of understory cover.

We were unable to find previous studies quantifying the amount of cover around Ruffed Grouse nest sites, and only Bump et al. (1947:128) gave a qualitative description. Apparent nest survival during their study was not affected by the density of undergrowth. Maxson (1978a), however, found higher apparent nest survival in mixed hardwoods, where a thick covering of ferns emerged during the incubation period, than in oak stands, where it did not. The amount of cover, quantified by several visual obstruction methods, did not appear to affect nest survival during our study. Bracken ferns (*Pteridium aquilinum aquilinum*) were not present when females selected their nest sites, but they provided much of the horizontal cover and ground cover at most nest sites subsequent to the nesting season and presumably during the later stages of incubation.

The proximity of grouse nests to a forest opening is thought to be significant for brood habitat immediately after chicks hatch (Maxson 1978a, Kimmel and Samuel 1984), not necessarily for nesting habitat. The distances to the nearest opening in our study are remarkably similar to the results from two other studies. Nearly 50% of all nests were within 10 m of an opening (Maxson 1978b), and

75% were within 30 m (Bump et al. 1947: 132–134). As expected, none of these studies revealed any association of distance to the nearest opening with nest survival. Distances from nests to the nearest mature aspen tree, the buds and leaves of which are important winter and early spring foods for Ruffed Grouse, also were similar between our study and others (Schladweiler 1968, Maxson 1978a).

Conclusions.—Our study suggests that survival of Ruffed Grouse nests is less than previously estimated. This may be a factor in declining grouse populations and the slow recovery of populations from low periods during the 10-year cycle observed in the northern part of their range. Increasing survival of first nests will have a much larger impact on grouse populations than a similar increase in survival of second nests due to differences in clutch size and egg hatching rates. Our study also outlines the wide range of habitat characteristics that may be successfully utilized by nesting Ruffed Grouse.

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HABITAT USE BY SWAINSON'S WARBLERS IN A MANAGED BOTTOMLAND FOREST

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ABSTRACT.—The Swainson's Warbler (*Limnothlypis swainsonii*) is a locally distributed and relatively uncommon Neotropical migrant songbird that breeds in the bottomland forests of the southeastern United States and spends the nonbreeding season in the Caribbean Basin. Populations of Swainson's Warblers have declined during recent decades as bottomland forests have come under increasingly intensive management and large areas have been converted to other land uses. We examined the habitat around song perches used by male Swainson's Warblers at Big Hammock Wildlife Management Area, a managed bottomland forest along the Altamaha River in Tattnall County, Georgia. We quantified 20 features of habitat structure in areas occupied by Swainson's Warblers (occupied plots) and two sets of controls: unoccupied plots adjacent to occupied plots (adjacent control plots) and unoccupied plots throughout the management area (general control plots). Occupied plots and adjacent control plots both differed in structure from the general control plots. We detected no significant differences, however, in vegetation structure between occupied plots and adjacent control plots. General control plots tended to have a greater number of trees, greater basal area, and a complete canopy, whereas occupied and adjacent control plots had high densities of small stems, cane, herbaceous ground cover, and leaf litter; this latter pattern is typical of documented Swainson's Warbler breeding habitat. Lack of significant differences in vegetation structure may be due to great variation in habitat structure around song perches, small sample size, or scarcity of Swainson's Warblers. Future research should focus on quantifying habitat characteristics around nest sites, song perches, and feeding areas. Our results suggest that management of bottomland habitats by thinning forests and encouraging regeneration of canebrakes is needed for successful conservation of Swainson's Warblers. *Received 14 October 2002, accepted 9 March 2003.*

The Swainson's Warbler (*Limnothlypis swainsonii*) is a locally distributed and relatively uncommon Neotropical migrant songbird that breeds in bottomland forests of the southeastern United States and spends the nonbreeding season in the Caribbean Basin (Meanley 1971, Brown and Dickson 1994). Populations of the Swainson's Warbler were suspected to be declining as early as 1971 (Meanley 1971), and a recent study indicated that the northernmost breeding populations in Maryland, Delaware, Missouri, and Illinois have disappeared during the last 30 years (Graves 2001). There is uncertainty about the status of Swainson's Warbler populations because standardized surveys (e.g., the Breeding Bird Survey) do not adequately sample Swainson's Warbler habitat. Thus, no strong correlations can be drawn about regional population trends. Nevertheless, greater numbers of Swainson's Warblers have been detected where they persist, but many local populations have become extirpated (Graves 2001).

Swainson's Warbler population declines have been attributed to habitat loss on both the breeding and wintering grounds (Graves 2001). On the breeding grounds, development of bottomland forests for other land uses (e.g., agriculture, reservoirs, pine plantations, housing development) has forced Swainson's Warblers into smaller patches of potentially less suitable habitat, which may affect breeding success and long term population persistence. Factors such as loss of breeding and wintering habitat, low population densities, and lack of information about breeding biology have contributed to making this species a top conservation priority (Hunter et al. 1993, Smith et al. 1993, Thompson et al. 1993).

Understanding the factors that influence reproductive success of Swainson's Warblers, such as habitat associations, is essential to developing appropriate conservation strategies for this species. In the southeastern portion of their breeding range, Swainson's Warblers

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typically are associated with well-shaded forested floodplains that contain dense undergrowth, including thickets, giant cane (*Arundinaria gigantea*), and semi-aquatic vegetation (Brewster 1885, Meanley 1971) interspersed with areas of little or no herbaceous ground cover (Meanley 1966, Eddleman et al. 1980, Thomas et al. 1996), and an extensive carpet of leaf litter overlying moist soils (Graves 1998). Thus, a suitable mosaic composition of the forest understory is thought to be more important to attracting Swainson's Warblers than the presence of a canebrake (Brown and Dickson 1994; Graves 2001, 2002). Specifically, dense areas are used for nesting and more open areas are used primarily for singing and foraging (Brown and Dickson 1994).

Breeding habitat appropriate for Swainson's Warblers historically was abundant in the extensive bottomland forests of the southeastern United States (Brantley and Platt 2001). As these forests have experienced increasingly intensive management for other land uses, the quality and availability of habitat have been reduced greatly (Meanley 1971, U.S. Dept. of the Interior 1993, Brown and Dickson 1994, Graves 2001) and probable breeding populations of Swainson's Warblers have been found in atypical habitats. For example, Swainson's Warblers recently were discovered in old growth bottomland forest fragments (see review in Graves 2001), a sweet gum (*Liquidambar styraciflua*) forest with a continuous understory of Chinese privet (*Ligustrum sinense*; SGS unpubl. data), and pine plantations with a deciduous understory (D. Roome pers. comm.). As a result, a quantitative analysis of the habitat within Swainson's Warbler territories is needed from managed forests, which are becoming an increasingly common feature of the environment. Furthermore, a quantitative comparison of occupied habitat to that generally available in managed forests is important for developing conservation strategies for Swainson's Warblers. The objective of this study was to conduct a quantitative analysis of habitat used by territorial male Swainson's Warblers in comparison to habitat in adjacent unoccupied areas and habitat generally available in a managed bottomland forest.

STUDY AREA AND METHODS

We conducted this study at Big Hammock Wildlife Management Area (BHWMA), a 2,605-ha area located on the northern shore of the Altamaha River in Tattnall County, Georgia (31° 50′ N, 82° 02′ W). BHWMA consists primarily of managed second growth bottomland hardwood forest with adjacent upland forest of varying age and forest type. The bottomland forest canopy is dominated by oak (*Quercus* spp.), sweet gum, ash (*Fraxinus* spp.), bald cypress (*Taxodium distichum*), and elm (*Ulmus* spp.). The understory includes American hornbeam (*Carpinus caroliniana*), red maple (*Acer rubrum*), river birch (*Betula nigra*), hawthorn (*Crataegus* spp.), holly (*Ilex* spp.), green briar (*Smilax* spp.), blackberry (*Rubus* spp.), and cane.

We surveyed BHWMA during 15 h of observation on 10 days from 12 May to 16 July 1999 by driving slowly (about 5 km/h) along a predetermined route, which allowed for an audible survey of a large portion of the bottomland forest in the management area. On two survey days we also walked two trails leading into areas we could not survey by vehicle. We visually located each singing male Swainson's Warbler (n = 12) and mapped the location of singing and foraging perches. We relocated all birds within their territories on at least three different days. We captured all 12 males using mist nets and song playbacks and we marked each bird with a USFWS aluminum leg band.

We quantified habitat structure using 11.3-m radius (0.045-ha) plots following James and Shugart (1970). We centered a plot on sites where each banded male repeatedly had been observed visiting and singing, for a total of 12 occupied plots. Because 11 of the 12 individual males were detected within 0.6 km of the Altamaha River (along a 3.3-km continuous stretch), we randomly selected 11 unoccupied plots along the river corridor that were adjacent to (but >250 m from) plots occupied by Swainson's Warblers (adjacent control plots). We used our map of known territories to determine potential adjacent control locations and used a coin and random numbers table to determine the side of the road and the distance (20–100 m) from the road where the plot would be located. The 12th random plot was

TABLE 1. Mean percentage of stems and basal area of some tree species varied significantly among occupied Swainson's Warbler territories (n = 12), adjacent control plots (n = 12), and general control plots (n = 12). Data were collected in the Big Hammock Wildlife Management Area, Tattnall County, Georgia, 1999.

	Occupied			Adjacent control			General control			P[a]	
Tree species	Stems	Basal area	Plots (n)	Stems	Basal area	Plots (n)	Stems	Basal area	Plots (n)	Stems	Basal area
Sweet gum, *Liquidambar styraciflua*	30.6	25.7	10	33.4	25.0	10	16.9	18.4	10	0.22	0.695
Water oak, *Quercus nigra*	13.6	15.7	6	0.5	0.1	1	0.8	0.7	1	0.01	0.013
American hornbeam, *Carpinus caroliniana*	12.2	7.0	8	26.8	17.8	8	9.9	4.3	6	0.19	0.155
Other spp.	8.4[b]	13.4	6	18.2[c]	26.9	9	10.0[d]	10.0	9	0.18	0.302
Laurel oak, *Q. laurifolia*	8.4	11.8	4	6.1	11.7	4	17.7	23.3	8	0.17	0.188
Willow oak, *Q. phellos*	7.4	12.0	4	5.7	7.6	5	18.7	22.3	10	0.13	0.174
Elms, *Ulmus* spp.	7.3	7.0	6	6.7	6.5	6	5.2	3.4	8	0.95	0.766
Ashes, *Fraxinus* spp.	5.9	5.3	2	0.6	1.1	1	6.5	5.4	6	0.13	0.155
Dead stems	4.9	3.4	5	0.0	0.0	0	8.5	7.8	9	0.002	0.003
Red maple, *Acer rubrum*	1.4	0.5	1	1.9	3.2	2	5.6	4.3	4	0.15	0.152

[a] Kruskal-Wallis ANOVA; Bonferroni adjustment: $P > 0.005$ not significant (0.05/10 = 0.005).
[b] *Nyssa sylvatica, Pinus taeda, Q. michauxii, Q. alba.*
[c] *P. taeda, Q. alba, Celtis laevigata, Cornus alternifolia, Crataegus* spp., *Betula nigra, Melia azedarach.*
[d] *Q. alba, Q. michauxii, B. nigra, Crataegus* spp., *Taxodium distichum, Acer negundo.*

near the one Swainson's Warbler located away from the river and was selected in a manner similar to the other plots. In general, we paired adjacent control plots with occupied plots. In addition, to allow a comparison of the habitat used by Swainson's Warblers to that generally available within BHWMA, we randomly selected 12 more plots (general control plots) on a grid of the entire management area, such that general control plots were >250 m from occupied or adjacent control plots. We gathered habitat structure data from August through September, 1999.

We measured size (dbh) of all woody stems ≥10 cm (trees) and identified each to species. We further categorized trees into six size classes for analysis: 10–14.9 cm, 15–19.9 cm, 20–29.9 cm, 30–44.9 cm, 45–59.9 cm, and >60 cm. We calculated mean basal area for each tree species. We quantified the number of shrub stems (<10 cm) per species along four 11.3 × 1.5-m belt transects and calculated stem density within each plot. We estimated percent canopy and herbaceous cover at 21 points (at about 2-m intervals) within each plot (one at the center and five points along each transect). We took five measures of litter depth at the first 2-m interval along each of the four transects and used mean litter depth for each plot in our analyses.

We used Kruskal-Wallis tests to evaluate differences in vegetation characteristics among plots because parametric assumptions were not met. Probabilities were Bonferroni adjusted for the number of simultaneous tests. We transformed habitat structure data using principal components analysis (PCA) and we compared individual PC scores among plot types with Kruskal-Wallis ANOVA. We used an orthogonal planned contrast to compare habitat along the Altamaha River (occupied and adjacent control plots) to that generally available at BHWMA (general control plots). We used a second orthogonal planned contrast to compare occupied plots to adjacent control plots to detect potential structural differences between occupied and unoccupied habitat. We set $\alpha = 0.05$ for all tests, and we analyzed all data using JMP 3.02 statistical software (SAS Institute, Inc. 1995).

RESULTS

The most common tree species, sweet gum, was distributed evenly across the three plot categories (Table 1). General control plots contained more dead trees than occupied and adjacent control plots. Occupied plots had more water oak (*Quercus nigra*) than adjacent control and general control plots.

Kruskal-Wallis ANOVA did not reveal significant differences in vegetation structure across plot types (Table 2). We used 20 vari-

ables in a principal components analysis to compare habitat structure among occupied, adjacent control, and general control plots. PC1 described a habitat gradient of large numbers of trees, basal area, and a complete canopy to habitat with an extensive litter layer, large percent herbaceous ground cover (i.e., grasses), and large numbers of cane, sweet gum, and other small stems. The gradient described by PC2 ranged from a large basal area of hornbeam, and large amounts of small trees/ha and herbaceous ground cover to areas with large sweet gum basal area, small stems and *Ilex* stems/ha. PC3 depicted a trend of large laurel (*Q. laurifolia*) and water oak basal area and number of large trees/ha to plots of large willow oak basal area, 30.0–49.9-cm trees/ha, and a large density of hornbeam stems. Vegetation structure differed significantly among plot categories along the first principal component axis (PC1: $F_{2,35} = 5.49$, $P = 0.009$), but we detected no significant differences along PC2 ($F_{2,35} = 0.90$, $P = 0.41$) or PC3 ($F_{2,35} = 0.33$, $P = 0.73$; Table 2).

DISCUSSION

Habitat structure in occupied and adjacent control plots was significantly different from the habitat generally available (general control plots) at BHWMA. General control plots typically were characterized as mature, open forest with relatively large numbers of trees and a complete canopy, which were features not typically associated with Swainson's Warblers (Brown and Dickson 1994, Graves 2001). In contrast, occupied plots and adjacent control plots were characterized by high densities of cane and small stems, and abundant leaf litter and herbaceous ground cover, all of which were structural characteristics associated with Swainson's Warblers at other locales (Brown and Dickson 1994; Graves 1998, 2001), and there was no detectable difference between the two plot types.

Stand history and flooding frequency and duration may explain differences in habitat structure among plots, as characterized by PC1. Areas that had evidence of prolonged flooding (i.e., the general control plots) tended to have many large trees and few small stems, which is not considered favorable Swainson's Warbler habitat (Graves 2001). The thick understory that describes occupied and adjacent control plots was due to less frequent and/or extensive flooding and increased canopy gaps from tree falls, which increased light availability and allowed thickets of cane and small stems to thrive. Thus, increased disturbance from tree falls provides for the development of suitable habitat for Swainson's Warblers (Graves 2002).

We found general differences in tree species composition and abundance among plot types. Compared to adjacent control plots, Swainson's Warblers were found in sites with greater amounts of water oak and tended to avoid high densities of American hornbeam and willow oak. Selection of water oak was noted for Swainson's Warblers at a breeding site in Louisiana (D. Roome pers. comm.). Graves (2001, 2002), however, found that Swainson's Warblers did not show selective use of specific floristic characteristics throughout the core breeding range of the species. Differences in floristic values between the general control plots and the occupied and adjacent control plots may be due to differences in the local hydrological gradient, which influences tree species composition. In addition, floristic values also may be related to the local stand history as the loss of canopy trees, through thinning or tree falls, facilitate the invasion of understory species.

Although our results generally agree with other descriptions of Swainson's Warbler habitat, the mean cane density we observed (1,748 stems/ha) around song perches was lower than that reported at another location in Georgia (50,000 stems/ha; Meanley 1971) or in Illinois (5,000 stems/ha; Eddleman et al. 1980). Occupied plots contained fewer trees relative to unoccupied habitat, but our large percent canopy closure (range 70–100%) was similar to the 85–90% canopy closure reported by Eddleman et al. (1980). In contrast to Eddleman et al. (1980) and Thomas et al. (1996), occupied plots at BHWMA had relatively high herbaceous ground cover (range 55–90%). Differences between this study and the literature may indicate that the species uses a larger range of forested habitats than previously known.

Although we measured numerous pertinent habitat variables, we did not detect differences in habitat structure between occupied and adjacent control plots. One explanation is that

TABLE 2. Habitat variables measured in occupied Swainson's Warbler territories (n = 12), adjacent control plots (n = 12), and general control plots (n = 12) did not differ significantly in univariate analyses, but the first principal component generated by these variables did differ significantly among plots. Data were collected in Big Hammock Wildlife Management Area, Tattnall County, Georgia, during 1999.

Variable	Mean values (range)		
	Occupied	Adjacent control	General control
Basal area (m^2/ha)			
American hornbeam, *Carpinus caroliniana*	0.8 (0–2.6)	1.5 (0–3.3)	0.7 (0–3.1)
Sweet gum, *Liquidambar styraciflua*	3.9 (0–12.6)	2.5 (0–11.9)	3.1 (0–10.9)
Laurel oak, *Quercus laurifolia*	2.1 (0–12.3)	2.4 (0–20.3)	6.4 (0–25.7)
Water oak, *Q. nigra*	2.1 (0–10.3)	0.0 (0–0.4)	0.0 (0–0.6)
Willow oak, *Q. phellos*	0.8 (0–5.9)	1.1 (0–6.6)	4.3 (0–22.1)
Other tree spp.	3.9 (0–8.0)	4.5 (0–20.5)	8.6 (0–34.1)
Tree density (stems/ha)			
Sweet gum, *Liquidambar styraciflua*	100 (0–688)	120 (0–821)	102 (0–955)
Holly, *Ilex* spp.	111 (0–466)	50 (0–488)	89 (0–311)
American hornbeam, *Carpinus caroliniana*	242 (0–1776)	285 (0–1621)	165 (0–1088)
10.0–14.9 cm dbh	141 (44–378)	115 (0–200)	224 (67–422)
15.0–19.9 cm dbh	85 (0–156)	80 (0–133)	117 (22–311)
20.0–29.9 cm dbh	74 (0–222)	39 (0–89)	109 (22–200)
30.0–44.9 cm dbh	44 (0–156)	28 (0–111)	61 (0–156)
45.0–59.9 cm dbh	6 (0–22)	11 (0–44)	11 (0–22)
>60 cm dbh	4 (0–22)	6 (0–44)	6 (0–44)
Other stem density (stems/ha)			
Shrubs	606 (44–1576)	865 (178–2730)	314 (66–710)
Cane, *Arundinaria* spp.	1748 (0–7747)	601 (0–2819)	163 (0–1443)
Percent cover			
Canopy	0.9 (0.7–1)	0.8 (0.4–1)	0.9 (0.6–1)
Herbaceous ground	0.6 (0.6–0.9)	0.6 (0.5–0.8)	0.5 (0.1–0.9)
Mean litter depth (cm)	1.9 (0.5–2.8)	2.3 (0.3–4.3)	1.3 (0.8–2.8)
Eigenvalue			
Percent variation explained			
Cumulative variation explained			

the mosaic of habitats that are utilized within territories may have produced too much variation in the data for relatively small differences to be detected (Brown and Dickson 1994; Graves 2001, 2002). Furthermore, our small sample size may have reduced our power for detecting structural differences between occupied and adjacent control plots. Alternatively, we suggest that at BHWMA there may be unoccupied sites suitable for territories. Although the density of Swainson's Warblers at our study area was comparable to that reported by Meanley (1971) from another locale in Georgia, there may not be enough Swainson's Warblers to fill the remaining unoccupied habitat.

In summary, our study quantified structural characteristics of Swainson's Warbler song perches and provides a general assessment of occupied habitat in a managed bottomland forest landscape in southeastern Georgia. Although our sample sizes were small, Swainson's Warbler habitat use seems to be highly specific. To better understand the habitat requirements of Swainson's Warblers, future research should focus on quantifying habitat structure around nesting sites, song perches, and other areas within territories. Furthermore, efforts should be directed at a comparative approach of estimating habitat use, territory size, and nest success in typical and atypical Swainson's Warbler habitats.

Nevertheless, if Swainson's Warbler is a conservation priority in the southeastern United States, we then suggest providing a combination of both dense canebrakes and open

TABLE 2. Extended.

Kruskal-Wallis ANOVA		Principal components factor loadings		
χ^2	P^a	PC1	PC2	PC3
2.4	0.294	0.0082	0.5257	−0.1343
0.6	0.754	0.0371	−0.3186	−0.0913
4.6	0.102	0.3294	−0.1722	0.3059
8.9	0.011	0.3294	−0.1722	0.3059
5.3	0.072	0.1119	−0.1521	−0.2383
3.2	0.055	0.2343	0.1869	−0.0808
2.7	0.253	−0.2848	−0.2658	−0.0088
4.5	0.105	0.0513	−0.2694	−0.1382
1.8	0.399	−0.1595	0.0951	−0.3717
5.9	0.052	0.2338	−0.0634	−0.0431
0.4	0.824	0.2557	0.2566	−0.1159
9.2	0.099	0.3141	0.0035	−0.1928
2.5	0.284	0.2247	−0.0068	−0.3082
1.6	0.455	0.1628	0.1036	0.2557
0.0	0.995	0.0969	0.1227	0.5165
5.4	0.068	−0.2848	0.0066	0.1645
9.9	0.007	−0.2026	0.1198	0.1083
4.6	0.101	0.2607	0.0518	0.0349
2.9	0.225	−0.2515	0.3013	0.2119
6.4	0.042	−0.2474	−0.1361	0.0353
		5.42	2.19	2.04
		27	11	10
		27	38	48

[a] Bonferroni adjustment: $P > 0.0025$ not significant (0.05/20 = 0.0025).

understory habitats for attracting breeding birds. Regenerating canebrakes through removing some large trees, while providing a minimum of 70% canopy closure after thinning, and planting cane may facilitate canebrake regeneration and may provide an important step in producing potentially suitable habitat for Swainson's Warblers (Eddleman et al. 1980, N. Klaus pers. comm.). Analysis of flooding regime and stand history (i.e., time since thinning, species of trees removed during thinning, tree falls) may provide insight into current and future canopy and understory composition and ultimately the production of potential Swainson's Warbler habitat. In addition, establishing a canebrake monitoring system would provide information about the presence of Swainson's Warblers across years (Eddleman et al. 1980). Ultimately, regenerating canebrakes in bottomland forests and monitoring nesting success in established and regenerated canebrakes is critical to understanding population dynamics of the Swainson's Warbler in the southeastern United States.

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BIRD COMMUNITIES IN THINNED VERSUS UNTHINNED SIERRAN MIXED CONIFER STANDS

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ABSTRACT.—We used point counts and nest monitoring to compare avian community composition and nesting success in thinned and unthinned stands of commercially managed Sierran mixed conifer forest. We conducted point counts and monitored 537 active nests of 37 species on 10 study plots during three consecutive breeding seasons in the northern Sierra Nevada. All 10 study plots had experienced a similar long term management history that included fire suppression and single-tree selection logging, but five of the plots also underwent a protocol of combined commercial and biomass thinning 5–8 years prior to the beginning of the study. Pooling species by nest substrate, we found that detections of ground-nesting bird species were similar on thinned and unthinned plots, but we detected canopy-, cavity-, and especially shrub-nesting species much more frequently on the thinned plots. Nest success rates were not statistically different between thinned and unthinned plots for ground-, shrub-, canopy-, or cavity-nesting species. Thinned stands were characterized by significantly less canopy cover, significantly lower density of small and medium conifers, and significantly greater understory cover and deer brush (*Ceanothus integerrimus*) cover than the unthinned stands. We surmise that the thinning protocol stimulated vigorous shrub growth, and conclude that forest conditions associated with a relatively open canopy and a well-developed shrub understory are highly beneficial to numerous breeding bird species in the Sierran mixed conifer community, including many species that may not nest or forage in the understory. Forest thinning that promotes vigorous shrub growth may correlate with an increased abundance of nesting birds, at least within stands affected by historical fire suppression and single-tree selection logging. *Received 1 October 2002, accepted 5 March 2003.*

Logging practices and human-altered fire regimes have changed forest structure and composition across much of the Sierra Nevada since the mid-Nineteenth Century (Franklin and Fites-Kaufmann 1996, Gruell 2001). Timber harvest practices and fire suppression throughout much of the region generally have reduced the frequency of low intensity fires, reduced the number of large trees, increased the density of smaller trees, and possibly reduced the extent of shrub cover (Weaver 1974, Vankat and Major 1978, McKelvey and Johnston 1992, Chang 1996). Concomitantly, forest composition has shifted substantially as altered fire regimes have favored the recruitment of shade tolerant tree species such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) at the expense of less shade tolerant pines (Agee et al. 1978, Bonnickson and Stone 1983, Weatherspoon et al. 1992, Chang 1996). These changes in forest structure and composition may have had far-reaching effects on avian community composition (Beedy 1982, Raphael et al. 1987, Hejl 1994), but adequate data for inferring historical avian community structure are lacking.

Across much of the Sierra Nevada, fuel loads resulting from decades of fire suppression have complicated the use of prescribed fire. If forest thinning can mimic at least some aspects of fire-induced ecological processes and forest structure, it may be an important tool for promoting wildlife species associated with the forest attributes that fire suppression discourages, especially in areas where land managers are reluctant to use prescribed fire. However, relatively little is known about the potential for silvicultural treatments to mimic the ecological functions of fire (Centers for Water and Wildland Resources 1996). Thinning protocols in Pacific Northwest second-growth forests have been shown to increase the abundance of breeding birds (Hagar et al. 1996) and other wildlife species (Sullivan et al. 2001) by promoting a more complex vertical stand structure. The limited information available from Sierran ecosystems, however, is inadequate for assessing whether biomass thinning—the removal of small-diameter, low value trees from dense stands—may effectively spur vigorous shrub growth, and thereby benefit shrub-associated bird species. While Sierran mixed conifer forest stands with rel-

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atively open canopies and well-developed shrub understories host higher densities of birds than stands with high canopy closure and poorly developed shrub understories (Beedy 1981), it remains to be established that biomass thinning can effectively produce these conditions, and if it can, that birds respond favorably.

Biomass thinning has been a common treatment on Sierran timberlands since the 1978 passage of the Public Utility Regulatory Policies Act, which created a market for the power generated by burning chipped trees (T. E. Kucera and R. H. Barrett unpubl. data). Biomass thinning has been implemented extensively across northern California's forests, with an estimated 24,000 ha of California forest thinned annually during the mid-1990s (T. E. Kucera and R. H. Barrett unpubl. data). In addition to generating extra income when energy market conditions are favorable, biomass thinning also may reduce the risk of fire reaching the forest canopy, may lower the competition among remaining trees for light, soil moisture and nutrients, and may increase the value of the wood products that ultimately can be harvested from the remaining trees (Helms and Tappeiner 1996, T. E. Kucera and R. H. Barrett unpubl. data). To the extent that the technique yields forest stands with relatively open canopies and well-developed shrub understories, it may increase the density of nesting birds, especially shrub-nesting species. Alternately, if the removal of small-diameter understory trees fails to stimulate vigorous shrub growth, it may have little effect, or even a negative effect, on shrub-associated bird species.

We compared breeding bird communities of thinned and unthinned stands of commercially managed, Sierran mixed conifer forest (Mayer and Laudenslayer 1988), where the historical management legacy included fire suppression and repeated stand entries for single-tree selection logging. We sought to ascertain how forest characteristics induced by combined commercial and biomass thinning correlate with avian community composition and nesting success in stands that had undergone these widely implemented management practices. We further sought to identify one or more simple, easily quantified habitat attributes associated with high densities of nesting birds or high levels of nest success. Such attributes could guide Sierra Nevada land managers interested in incorporating the habitat needs of breeding birds into their forest management plans.

STUDY AREA AND METHODS

Study area.—We worked on Sierra Pacific Industries timberlands in Tehama County, California, on the western slope of the Sierra Nevada. Our 10 study plots were dominated by Sierran mixed conifer forest, comprised of varying proportions of white fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), incense cedar, and sugar pine (*P. lambertiana*), with occasional small stands and single individuals of California black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepis*), as well as mountain dogwood (*Cornus nuttallii*), bigleaf maple (*Acer macrophyllum*) and California hazelnut (*Corylus cornuta*). Deer brush (*Ceanothus integerrimus*) was the dominant understory shrub, but other common shrubs included mahala mat (*C. prostratus*), creeping snowberry (*Symphoricarpos acutus*), Sierra gooseberry (*Ribes roezlii*), and to a lesser extent, greenleaf manzanita (*Arctostaphylos patula*), poison-oak (*Rhus diversiloba*), and Sierra chinquapin (*Castanopsis sempervirens*). All 10 plots were primarily south facing, with mean slopes ranging from 5–15°.

Study design and sampling.—During the spring of 1998 we identified two patches of forest on nearby, roughly parallel south-facing slopes that were similar in aspect, slope, forest type, and seral stage, but differed in that a protocol involving both biomass thinning and commercial thinning (single tree selection) was applied to one of them between 1990 and 1993 (different portions of the slope were thinned during different years). The thinning treatment involved removing some individually selected merchantable trees (commercial thinning) as well as smaller trees and saplings (biomass thinning) to retain vigorous, healthy trees spaced approximately 8.2 m apart (S. Self pers. comm.). Both patches had undergone similar histories of previous silviculture treatments. The patch that was thinned during the early 1990s underwent selection overstory logging during the late 1930s and early 1940s, again between 1978 and 1988, and once more

in a small area during 1994. The unthinned patch, about 5 km to the northwest, underwent similar overstory logging during the late 1950s and again during 1978 and 1994.

We established five 36-ha study plots in each patch by randomly selecting starting points on maps of the two areas of interest, and then extending boundaries out in random cardinal directions. Boundaries were turned 90° when they approached within 200 m of another plot, or within 100 m of a riparian buffer area that had been managed differently than the upland forest. The resulting thinned plots (centered on 40° 07′ N, 121° 34′ W) were located at 1,250–1,430 m elevation, similar to the unthinned plots (centered on 40° 11′ N, 121° 35′ W), which were located at 1,160–1,550 m elevation. We stress that historical overstory logging occurred previously on both sets of plots, so our unthinned plots were unthinned only in the sense that they did not undergo the 1990s biomass and commercial thinning treatment.

To ensure that we devoted equal effort to nest searching on thinned and unthinned plots and avoided bias from uneven observer abilities, field crews alternated days searching for nests on the thinned plots and unthinned plots. We searched for nests according to the guidelines in Martin and Geupel (1993), and recorded nest observations and habitat data in accordance with standard nest-monitoring guidelines described in Martin et al. (1997). Once we discovered an active nest, we visited it at least once every four days, but usually every two days. We considered nests successful if they fledged at least one young bird. We based nest fate determinations on nesting intervals described in Ehrlich et al. (1988), and the criteria described in Manolis et al. (2000), which provide standardized guidelines for determining whether nests succeeded, and for incorporating nests with uncertain fates into analyses.

We conducted point counts three times in each of three years (1998–2000) between 23 May and 18 June at nine points (hereafter a transect) on each study plot. Nine points, the maximum number that we could fit on each plot while still ensuring that points were spaced 200 m apart, were arrayed in a regular grid and were ≥100 m from the plot boundary. Each year three observers trained in bird identification conducted all the point count surveys, such that each replicate was conducted by a different observer, and all 10 plots were surveyed by the same three observers. Point counts began within 10 min of official local sunrise and generally were completed by 09:00. The order of points was shifted for each repeated survey so that each point was surveyed once each year during the early, middle, and later part of the morning. Point counts were not conducted on mornings with rain or enough wind to generate substantial noise interference. Each point count lasted 5 min, during which observers noted every bird seen or heard, and recorded birds detected within a 50-m radius separately from birds detected beyond 50 m. Only birds detected within the 50 m radius were included in the analysis of bird communities. When observers detected individual birds they believed had been detected from a previous point on the same day (generally very loud species that could be heard calling from the same area at two consecutive point count stations), they noted them as such, and we included only the first detection in our analysis.

While we support recent calls for researchers to utilize distance sampling or some other means of correcting point count data for detectability (Rosenstock et al. 2002, Williams et al. 2002), we believe our use of a 50-m detection radius was sufficient to safeguard against spurious results. In another study of unthinned Sierran forest involving many of the same species present on our plots, DeSante (1986) determined that basal detection radii (distance band from the observer within which distance from the observer to a bird is unrelated to detection probability) for most species well exceeded 50 m. Nevertheless, to test for potentially confounding variation in the detection function between our two sets of plots, we used a 2×2 contingency table to compare the ratio of the number of birds detected within 50 m of the observer to the number of birds detected beyond 50 m from the observer on thinned and unthinned plots (Buckland et al. 2001). If detectability was greater on the thinned plots compared to the unthinned plots, we would expect that the proportion of all detections that were beyond 50 m of the observer would be greater on the thinned plots than on the unthinned plots. We

TABLE 1. The five thinned Sierra forest plots exhibited less canopy cover, lower density of small and medium conifers, and greater deer brush cover and overall understory cover than the five unthinned plots. Other habitat variables we examined were similar across both plot types. Values are mean ± SD. Data are from northern California, 1998–2000.

Habitat variable	Thinned plots	Unthinned plots	*t*	*P*
Canopy cover (%)	53.0 ± 7.0	66.3 ± 7.4	2.6	0.032
Canopy height (m)	23.3 ± 1.5	21.4 ± 2.5	1.3	0.233
Understory cover (%)	27.2 ± 7.0	17.6 ± 2.2	2.7	0.029
Deer brush cover (%)	15.4 ± 3.4	4.7 ± 3.0	4.8	0.001
Oak density (trees/ha)	12.5 ± 15.4	22.3 ± 18.4	0.8	0.437
Large conifer density (trees/ha)	74.2 ± 9.0	77.7 ± 13.6	0.4	0.683
Medium conifer density (trees/ha)	91.4 ± 33.8	182.0 ± 24.0	4.4	0.002
Small conifer density (trees/ha)	97.4 ± 70.8	329.7 ± 124.0	3.3	0.012
Snag density (trees/ha)	15.8 ± 14.4	19.7 ± 3.6	0.5	0.614

know of no previously published studies examining the effects of forest thinning on bird detectability.

We collected habitat data between 1998 and 2000 in accordance with the guidelines provided by Martin et al. (1997). This involved assessing vegetation structure and composition within 5.0-m radius subplots (for shrubs, saplings, and ground cover) and 11.3-m radius subplots (for trees and snags) at 36 points (12 each year) in a systematic array covering each of the 10 study plots. Within each vegetation subplot, we measured canopy cover with a spherical densiometer, measured canopy height with a clinometer, counted the number of small (<23 cm dbh), medium (23–38 cm dbh) and large (>38 cm dbh) conifers, counted the number of oaks and the number of snags (≥2 m tall), and visually estimated the percent cover provided by deer brush (the most abundant shrub species on the study plots), and the percent cover provided by all woody plants <5 m tall (hereafter the understory component of the forest). Although Block et al. (1987) showed that visual cover estimates can vary substantially among observers, our sampling design insured that each observer sampled an equal number of subplots on both the thinned plots and the unthinned plots. We considered trees <5 m tall or <8 cm dbh to be saplings, and did not include them in tree density estimates, although they did contribute to the understory percent cover. For each habitat variable, we averaged values from the 36 subplots to produce a single plot-wide mean for each of the 10 study plots.

Data analysis.—In accordance with recent guidelines proposed by Manolis et al. (2000), our calculation of nest success rates incorporates nests with uncertain fates, with exposure terminated on the last observed active date. We assumed nests with known fates terminated at the midpoint between the last observed active date and the first observed inactive date (Manolis et al. 2000).

We pooled nest success data across species within each of four groups of birds: ground-nesting, shrub-nesting, canopy-nesting, and cavity-nesting species. For each group we calculated daily nest success rates on the thinned plots and the unthinned plots, using the methods of Mayfield (1961, 1975). We used *t*-tests to compare point count detections of each group on thinned and unthinned plots, and to compare habitat attributes of thinned and unthinned plots. We used χ^2 tests with Yates correction for continuity to assess whether the numbers of nests of each species or group of species on thinned versus unthinned plots differed from the expected 1:1 ratio. The significance threshold for all statistical tests was $P < 0.05$, and all tests were two tailed. We used SYSTAT (SPSS, Inc. 1997) to perform all statistical tests.

RESULTS

General plot characteristics.—Compared to unthinned plots, thinned plots exhibited significantly lower canopy cover, medium conifer density, and small conifer density, and significantly higher understory cover and deer brush cover (Table 1). Among the nine habitat variables we examined, deer brush cover differed most strongly between the two sets of

plots (Table 1). Understory cover was negatively correlated with canopy cover ($r^2 = 0.42$, $P = 0.044$), as was deer brush cover ($r^2 = 0.63$, $P = 0.006$). Canopy height, oak density, large conifer density, and snag density were statistically equivalent on the two sets of plots (Table 1).

Point counts.—During nine point count transects (three replicates during each of three years), we recorded 44 bird species on the thinned plots, 39 of which also were recorded on the unthinned plots; no bird species were detected on the unthinned plots only. Of those 44 species, significantly more of them (32) were detected more frequently on the thinned plots than on the unthinned plots ($\chi^2 = 8.2$, df = 1, $P = 0.003$).

Excluding species whose nests we never found on any of the 10 study plots, we detected a mean of 48.6 individual birds per transect on the thinned plots compared to 31.0 birds per transect on the unthinned plots ($t = 7.08$, df = 8, $P = 0.0001$; Table 2). Thinned plot and unthinned plot detection totals of ground-nesting species were not statistically different ($t = 0.09$, df = 8, $P = 0.93$; Table 2), but thinned plot totals were much higher than unthinned plot totals for pooled shrub-nesting species ($t = 3.69$, df = 8, $P = 0.006$; Table 2), pooled canopy-nesting species ($t = 4.61$, df = 8, $P = 0.002$; Table 2), and pooled cavity-nesting species ($t = 3.80$, df = 8, $P = 0.005$; Table 2).

Pooling all species, we recorded 51.1% of bird detections beyond 50 m of the observer on the thinned plots, compared to 58.6% on the unthinned plots ($\chi^2 = 58.9$, df = 1, $P < 0.0001$).

Nest monitoring.—The number of active nests we found on individual study plots correlated significantly with the mean number of point count detections of species we found nesting on at least one of the 10 study plots ($r^2 = 0.85$, $P = 0.0002$). We found 537 active nests on the 10 study plots; 139 (26%) were located on the unthinned plots, and 398 (74%) were located on the thinned plots (Table 3). Nest totals on the thinned plots were significantly higher than on the unthinned plots for ground-nesting species ($\chi^2 = 14.1$, df = 1, $P = 0.0004$), shrub-nesting species ($\chi^2 = 86.4$, df = 1, $P < 0.0001$), canopy-nesting species ($\chi^2 = 10.9$, df = 1, $P = 0.0007$), and cavity-nesting species ($\chi^2 = 27.5$, df = 1, $P < 0.0001$; Fig. 1a), as well as for all species pooled ($\chi^2 = 124.0$, df = 1, $P < 0.0001$).

We determined the fate of 470 of the 537 active nests we observed (Table 3). We observed significantly more successful nests of shrub-nesting species ($\chi^2 = 35.8$, df = 1, $P < 0.0001$), canopy-nesting species ($\chi^2 = 5.78$, df = 1, $P = 0.011$), and cavity-nesting species ($\chi^2 = 8.49$, df = 1, $P = 0.002$) on the thinned plots (Fig. 1b). Although we found nearly twice as many ground nests on the thinned plots as compared to the unthinned plots (Fig. 1a), the difference in numbers of successful nests was not statistically significant ($\chi^2 = 3.45$, df = 1, $P = 0.067$). We observed successful nests of four individual species in significantly greater numbers on the thinned plots than on the unthinned plots: Dark-eyed Junco (*Junco hyemalis*; $\chi^2 = 4.36$, df = 1, $P = 0.024$), Dusky Flycatcher (*Empidonax oberholseri*; $\chi^2 = 21.0$, df = 1, $P < 0.0001$), Hammond's Flycatcher (*Empidonax hammondii*; $\chi^2 = 8.10$, df = 1, $P = 0.002$), and Black-headed Grosbeak (*Pheucticus melanocephalus*; $\chi^2 = 7.11$, df = 1, $P = 0.004$). We observed no species with significantly more successful nests on the unthinned plots.

On both the thinned and the unthinned plots, cavity-nesters had relatively high daily nest success, shrub and canopy nesters had intermediate nest success rates, and ground-nesters had the lowest nest success rates (Fig. 1c). There was a nonsignificant tendency for ground, canopy, and cavity nests on unthinned plots to succeed at greater rates than those on thinned plots, but differences in daily nest success rates were not statistically different between thinned and unthinned plots for any of the four groups of species (Fig. 1c).

DISCUSSION

Our finding that a significantly greater proportion of birds were detected beyond 50 m of the observer on the unthinned plots than on the thinned plots does not support the hypothesis that detectability was greater on the thinned plots. The great majority of point count detections in forested habitat are generally auditory, rather than visual, and the proportion of auditory detections increases with distance from observer. The increased shrub cover on the thinned plots may have reduced

TABLE 2. We detected most shrub-, canopy- and cavity-nesting species much more frequently on thinned plots than on un-thinned plots, while ground-nesting species were recorded at relatively similar frequencies on the two sets of plots. Detections per transect indicates the mean number of birds detected within a 50-m radius during nine replicates (three replicates during each breeding season) of each point count transect. Each point count transect comprised nine point counts. Results are presented for species with at least one nest found on any of the study plots. Values are mean ± SD. Data are from northern California, 1998–2000.

Species	Detections per transect	
	Unthinned plots	Thinned plots
Ground-nesting species		
Mountain Quail (*Oreortyx pictus*)	0.20 ± 0.22	0.13 ± 0.13
Townsend's Solitaire (*Myadestes townsendi*)	0.38 ± 0.17	0.15 ± 0.05
Nashville Warbler (*Vermivora ruficapilla*)	2.42 ± 0.99	0.82 ± 0.77
Spotted Towhee (*Pipilo maculatus*)	1.40 ± 0.63	1.38 ± 0.54
Dark-eyed Junco (*Junco hyemalis*)	3.82 ± 0.97	5.02 ± 0.62
Fox Sparrow (*Passerella iliaca*)	0.35 ± 0.19	1.16 ± 0.92
Pooled	8.57 ± 1.63	8.66 ± 1.25
Shrub-nesting species		
Dusky Flycatcher (*Empidonax oberholseri*)	0.07 ± 0.09	5.98 ± 1.92
Hermit Thrush (*Catharus guttatus*)	0.13 ± 0.16	0.36 ± 0.36
Cassin's Vireo (*Vireo cassinii*)	1.49 ± 0.42	3.04 ± 0.67
Yellow Warbler (*Dendroica petechia*)	0.11 ± 0.10	0.46 ± 0.44
MacGillivray's Warbler (*Oporornis tolmiei*)	0.11 ± 0.07	0.29 ± 0.13
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1.58 ± 0.57	1.16 ± 0.52
Lazuli Bunting (*Passerina amoena*)	1.86 ± 0.45	1.13 ± 0.59
Chipping Sparrow (*Spizella passerina*)	0.24 ± 0.04	0.80 ± 0.36
Pooled	5.59 ± 0.66	13.22 ± 4.08
Canopy-nesting species		
Anna's Hummingbird (*Calypte anna*)	0.02 ± 0.04	0.27 ± 0.42
Calliope Hummingbird (*Stellula calliope*)	0.00 ± 0.00	0.04 ± 0.09
Western Wood-Pewee (*Contopus sordidulus*)	0.07 ± 0.09	0.18 ± 0.15
Hammond's Flycatcher (*Empidonax hammondii*)	0.11 ± 0.12	2.58 ± 0.18
Steller's Jay (*Cyanocitta stelleri*)	1.42 ± 0.69	0.53 ± 0.28
American Robin (*Turdus migratorius*)	0.22 ± 0.27	0.49 ± 0.18
Warbling Vireo (*Vireo gilvus*)	0.13 ± 0.13	1.11 ± 0.76
Yellow-rumped Warbler (*Dendroica coronata*)	2.89 ± 0.52	4.40 ± 0.61
Black-throated Gray Warbler (*Dendroica nigrescens*)	0.51 ± 0.39	0.07 ± 0.09
Hermit Warbler (*Dendroica occidentalis*)	2.67 ± 0.92	4.42 ± 0.65
Western Tanager (*Piranga ludoviciana*)	3.96 ± 1.01	4.16 ± 0.54
Purple Finch (*Carpodacus purpureus*)	0.09 ± 0.18	0.04 ± 0.05
Evening Grosbeak (*Coccothraustes vespertinus*)	0.04 ± 0.09	0.22 ± 0.23
Pooled	12.13 ± 2.16	18.49 ± 1.71
Cavity-nesting species		
Northern Flicker (*Colaptes auratus*)	0.24 ± 0.15	0.60 ± 0.21
White-headed Woodpecker (*Picoides albolarvatus*)	0.15 ± 0.15	0.53 ± 0.18
Red-breasted Sapsucker (*Sphyrapicus ruber*)	0.07 ± 0.09	0.31 ± 0.26
Hairy Woodpecker (*Picoides villosus*)	0.20 ± 0.19	0.45 ± 0.24
Pileated Woodpecker (*Dryocopus pileatus*)	0.13 ± 0.13	0.02 ± 0.04
Mountain Chickadee (*Poecile gambeli*)	1.47 ± 0.83	2.89 ± 0.52
Red-breasted Nuthatch (*Sitta canadensis*)	1.51 ± 0.33	2.00 ± 0.16
Brown Creeper (*Certhia americana*)	0.93 ± 0.63	1.38 ± 0.96
Pooled	4.70 ± 1.52	8.18 ± 1.01
All nesting species pooled	31.00 ± 2.38	48.55 ± 4.34

TABLE 3. Number of nests of each species found on unthinned and thinned plots (followed by number of nests with known fates in parentheses), and number of successful nests observed on unthinned and thinned plots. Species with significantly more nests found on the thinned plots than on the unthinned plots are indicated in bold type; no species' nests were found significantly more often on the unthinned plots. Data are from northern California, 1998–2000.

	Unthinned plots		Thinned plots	
	All nests	Successful nests (%)	All nests	Successful nests (%)
Ground-nesting species				
Mountain Quail	0 (0)	0 (0.0)	2 (2)	0 (0.0)
Townsend's Solitaire	4 (4)	2 (50.0)	7 (7)	3 (42.9)
Nashville Warbler	2 (2)	2 (100)	0 (0)	—
Spotted Towhee	6 (6)	3 (50.0)	7 (7)	3 (42.9)
Dark-eyed Junco	**22 (22)**	**10 (45.5)**	**51 (50)**	**23 (46.0)**
Fox Sparrow	0 (0)	0 (0.0)	7 (7)	2 (28.6)
Shrub-nesting species				
Dusky Flycatcher	**0 (0)**	—	**76 (67)**	**23 (34.3)**
Hermit Thrush	1 (1)	0 (0.0)	4 (4)	2 (50.0)
Cassin's Vireo	10 (8)	3 (37.5)	22 (21)	9 (42.9)
Yellow Warbler	0 (0)	—	6 (6)	4 (66.7)
MacGillivray's Warbler	0 (0)	—	2 (2)	2 (100)
Black-headed Grosbeak	1 (1)	0 (0)	16 (16)	9 (56.3)
Lazuli Bunting	10 (10)	6 (60.0)	6 (6)	4 (66.7)
Chipping Sparrow	0 (0)	—	10 (6)	5 (83.3)
Canopy-nesting species				
Sharp-shinned Hawk	1 (0)	0 (0.0)	0 (0)	—
Northern Goshawk	1 (1)	0 (0.0)	0 (0)	—
Anna's Hummingbird	1 (1)	0 (0.0)	2 (2)	1 (50.0)
Calliope Hummingbird	2 (2)	2 (100)	0 (0)	—
Western Wood-pewee	0 (0)	—	1 (1)	1 (100)
Hammond's Flycatcher	**1 (0)**	**0 (0.0)**	**19 (16)**	**10 (62.5)**
Steller's Jay	3 (2)	1 (50.0)	0 (0)	—
American Robin	6 (5)	2 (40.0)	5 (5)	0 (0.0)
Warbling Vireo	**1 (1)**	**1 (100)**	**22 (19)**	**6 (31.6)**
Yellow-rumped Warbler	8 (7)	2 (28.6)	17 (13)	9 (69.2)
Black-throated Gray Warbler	4 (2)	1 (50.0)	0 (0)	—
Hermit Warbler	4 (3)	2 (66.7)	6 (4)	2 (50.0)
Western Tanager	20 (18)	5 (27.8)	21 (18)	5 (27.8)
Purple Finch	1 (0)	0 (0.0)	0 (0)	—
Evening Grosbeak	0 (0)	—	1 (1)	0 (0.0)
Cavity-nesting species				
Northern Flicker	4 (4)	3 (75.0)	12 (9)	3 (33.3)
White-headed Woodpecker	**2 (2)**	**2 (100)**	**12 (11)**	**7 (63.6)**
Red-breasted Sapsucker	**0 (0)**	—	**11 (9)**	**7 (77.8)**
Hairy Woodpecker	1 (1)	0 (0.0)	4 (4)	3 (75.0)
Pileated Woodpecker	1 (1)	1 (100)	0 (0)	—
Mountain Chickadee	**4 (3)**	**1 (33.3)**	**19 (14)**	**6 (42.9)**
Red-breasted Nuthatch	**8 (5)**	**3 (60.0)**	**21 (16)**	**11 (68.8)**
Brown Creeper	10 (9)	7 (77.8)	9 (6)	3 (50.0)
All Species	**139 (121)**	**59 (48.8)**	**398 (349)**	**163 (46.7)**

the visual detectability of birds, particularly those near the observer (i.e., within 50 m). Therefore, the true differences in bird abundances between the two sets of plots may be even greater than we report.

Except for shrub-nesting species, avian community composition was similar for thinned and unthinned plots, but over 1.5 times as many birds were detected on the thinned plots. Nest-finding and point count

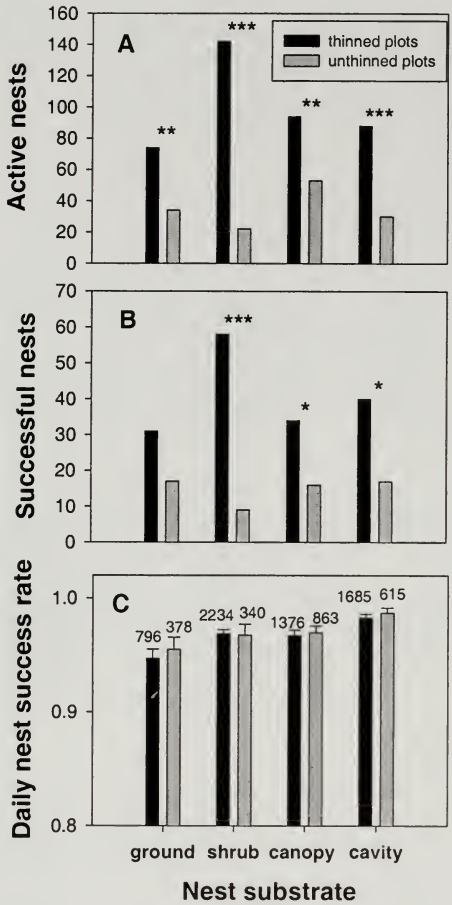

FIG. 1. We observed many more (a) active nests and (b) successful nests on thinned plots than on unthinned plots. Daily nest success rates (c) of thinned and unthinned plots were indistinguishable. Numbers above error bars indicate the number of observation days on which each success rate is based. * indicates $P < 0.05$, ** indicates $P < 0.001$, and *** indicates $P < 0.0001$.

data both corroborate that shrub, canopy, and cavity-nesting species occurred on the thinned plots at much higher densities than on the unthinned plots. Results for ground-nesting species were slightly more ambiguous. Point count data suggest that ground-nesting species were equally abundant on thinned and unthinned plots, but we found significantly more ground nests on the thinned plots than on the unthinned plots. Of course, nest-searching results must be interpreted with some caution, as they also could be biased by differences in detectability between the thinned and unthinned plots. Still, it seems very unlikely that any such differences could have been of high enough magnitude to explain our finding nearly three times as many nests (all species pooled) on the thinned plots (Table 3).

The difference in bird communities between the thinned and unthinned plots was most extreme among shrub-nesting species. Dusky Flycatchers, the single most commonly detected species on the thinned plots (mean of 29.89 detections per point count transect; 76 nests found), were virtually absent from the unthinned plots (mean of 0.33 detections per point count transect; no nests found). Except for Black-headed Grosbeak and Lazuli Bunting (*Passerina amoena*), we detected each of the nine shrub-nesting species we found nesting on one or more of the study plots at least twice as often on the thinned plots as on the unthinned plots.

The thinning protocol was implemented between 1990 and 1993, 5–8 years before the beginning of our study, and 8–11 years before the end. Although we did not quantify shrub cover before the forest was thinned, comparison with the unthinned plots suggests that thinning successfully stimulated vigorous shrub growth, which was then associated with elevated densities of birds. While this makes intuitive sense for shrub-nesting species, it is less clear why canopy and cavity-nesting species would be more abundant on thinned plots with substantially greater shrub cover. For birds with life histories less tied to shrubs, extent of the shrub layer may be a proxy for other ecological variables with which it correlates, rather than a direct causal factor. Hammond's Flycatchers, for example, forage on flying insects by sallying into the open spaces beneath the overstory canopy and between trees (Mannan 1984, Hagar et al. 1996). This species may therefore be responding to the increased space available for foraging underneath the canopy, rather than the increase in the extent of shrubs, although increased shrub growth likely results from the same conditions that produce good Hammond's Flycatcher foraging habitat.

Even species such as Golden-crowned Kinglets (*Regulus satrapa*) and Brown Creepers (*Certhia americana*), which usually are associated with mature, shaded forest stands (Ziener et al. 1990) did not appear to be substan-

tially negatively impacted by the thinning. Both species were relatively common on thinned as well as unthinned plots, with statistically indistinguishable numbers of detections in the two plot types. We were unable to locate any kinglet nests, but found virtually identical numbers of Brown Creeper nests on thinned plots (9 nests) and unthinned plots (10 nests).

While nesting density differed substantially between the two sets of plots, nest success rates did not. Although pooling nest success data by nesting group could potentially mask poor nesting success of particular species (Mannan et al. 1984), generating adequate sample sizes for studying nest success rates of more than a few species is notoriously difficult. Reliable estimates of species specific nest success rate generally require at least 20 nests (Hensler and Nichols 1981), and in many cases even 20 nests are far from adequate for detecting differences in nest survivorship between two groups (Nur et al. 1999). Where such large single species sample sizes are unavailable, pooling species by nesting group or other shared characteristics can provide an important function. Alarmingly low nest success rates of groups of species with similar nesting habits or other shared characteristics can signal researchers to target the constituent species for more intensive study, of the sort that might generate the large sample sizes needed for species specific estimates.

Brown-headed Cowbirds (*Molothrus ater*) were detected in low numbers on the thinned plots, and virtually never on the unthinned plots. During the three years of this study, we confirmed cowbird parasitism at six nests, including three Cassin's Vireo (*Vireo cassinii*) nests, two Warbling Vireo (*Vireo gilvus*) nests, and one Yellow-rumped Warbler (*Dendroica coronata*) nest. While such a small sample size prevents any firm conclusions, all six parasitized nests were located on the thinned plots, raising the possibility that forest openings created by the thinning protocol may have made nesting songbirds more vulnerable to cowbird parasitism.

Overall, nests on unthinned plots exhibited slightly higher success rates than nests on thinned plots, but the differences were not significant. Even if real, the differences were not large enough to compensate for the comparatively low density of shrub, canopy, and cavity nesters on unthinned plots; the thinned plots clearly produced more fledglings than did the unthinned plots.

The fact that our results come from just two clusters of study plots on adjacent slopes limits our ability to extrapolate our findings to other parts of the Sierra Nevada, or to pin down a definitive causal relationship between silviculture treatments and avian community composition. Nevertheless, our results suggest that forest conditions which stimulate vigorous shrub growth, particularly growth of deer brush, may be highly beneficial to the majority of breeding birds in the Sierran mixed conifer community, even if the precise ecological mechanisms for canopy- or cavity-nesting species remain obscure. Multispecies management is usually a balancing act among the conflicting needs of different species of concern. The combination of commercial and biomass thinning on our study plots appears to have provided a rare exception to the general rule that habitat attributes benefiting some species of concern are detrimental to others. Even birds normally thought of as forest interior species, such as Brown Creepers and Golden-crowned Kinglets, did not appear to be deleteriously affected by the thinning, while many species may have benefited. If our results hold true across the larger Sierran landscape, then thinning that promotes the growth of deer brush and other shrubs in Sierran mixed conifer stands affected by historical fire suppression may be a useful tool for enhancing habitat value for forest-nesting birds, at least during the breeding season. We stress, however, that these results do not necessarily imply that forest thinning will increase nesting bird density in stands that have experienced more natural fire regimes. Rather, our results suggest that thinning practices that spur shrub growth may be valuable for enhancing the habitat value of forest stands comprising densely packed, stunted conifers, and very few shrubs.

Finally, detectability estimation methods such as distance sampling (Buckland et al. 2001), the double-observer approach (Nichols et al. 2000), or double sampling (Bart and Earnst 2002) should be incorporated into study designs whenever feasible. Our comparison of the ratios of the number of detec-

tions <50 m and >50 m from the observer may be a useful technique for researchers interested in determining the potential value of data sets based on limited radius point counts but with no adjustments for detectability.

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MIGRATION ROUTES AND WINTERING LOCATIONS OF BROAD-WINGED HAWKS TRACKED BY SATELLITE TELEMETRY

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ABSTRACT.—During spring 2000, we captured five adult female Broad-winged Hawks (*Buteo platypterus*) in northcentral Minnesota and western Maryland and fitted them with satellite-received radio tags. The migrating hawks left their nesting areas about 10–15 September and moved south toward eastern Texas. They followed the Gulf Coast through Mexico and an inland course through Central America to their wintering areas. Mean fall migration distance for four hawks was about 7,000 km, and for three hawks the mean fall migration time was about 70 days and mean fall migration rate was about 100 km/day. Three hawks arrived on their wintering areas from about 15 October to 15 December. Wintering areas for four hawks were in Panama, Venezuela, Brazil, and Peru, between 08° 25′ N, 80° 54′ W and 11° 00′ S, 67° 07′ W. We tracked one hawk for her entire spring migration, and two hawks showed fidelity to their nest areas. *Received 5 October 2002, accepted 17 March 2003.*

Little information has been published about migration routes, timing, or wintering sites of the Broad-winged Hawk (*Buteo platypterus*; Goodrich et al. 1996). Observational and banding return data show that the species' winter range extends from southern Mexico into Central America and middle South America, with small numbers wintering in Florida (Goodrich et al. 1996).

Satellite-received radio tags (platform transmitter terminals, or PTTs) have allowed biologists to monitor the movements of Neotropical migrants such as Ospreys (*Pandion haliatus*; Martell et al. 2001), Peregrine Falcons (*Falco peregrinus*; Fuller et al. 1998, McGrady et al. 2002), and Swainson's Hawks (*Buteo swainsoni*; Fuller et al. 1998), providing new insights into these species' migratory and winter habits, and valuable data for their management and conservation. The objective of this study was to better understand the migratory movements of Broad-winged Hawks and to identify the wintering areas of birds from known nesting areas.

METHODS

We captured five breeding adult female Broad-winged Hawks at their nesting sites using a mist net and a Great Horned Owl (*Bubo virginianus*) as a lure (Matray 1974) during June 2000, in western Maryland (39° 37′ N, 79° 13′ W) and northcentral Minnesota (46° 37′ N, 94° 14′ W; Fig. 1). We fitted them with 20-g PTTs (Northstar Science and Technology, Baltimore, Maryland), attaching them as backpacks using Teflon ribbon sewn with cotton thread that would break down over time (Britten et al. 1999).

We harnessed PTT numbers MN97, MN61, and MN88 to birds in Minnesota and numbers MD93 and MD95 to birds in Maryland. All hawks weighed between 445 and 475 g; thus, the PTTs were approximately 4% of the birds' body mass, similar to that of other studies using radio transmitters (Pennycuick et al. 1989, Vekasy et al. 1996, Marzluff et al. 1997, Fuller et al. 1998, Britten et al. 1999, Kenward 2001, and McGrady et al. 2002). We programmed the PTTs to transmit 6 h on and 246 h off during the 2000 summer season (7 cycles over 70 days), for 6 h on and 38 h off during fall migration (38 cycles over 60 days), and 6 h on and 80 h off throughout winter or until battery failure.

We located the hawks using NOAA satellites with onboard tracking equipment operated by ARGOS Inc. The data received from ARGOS included estimation of latitude and

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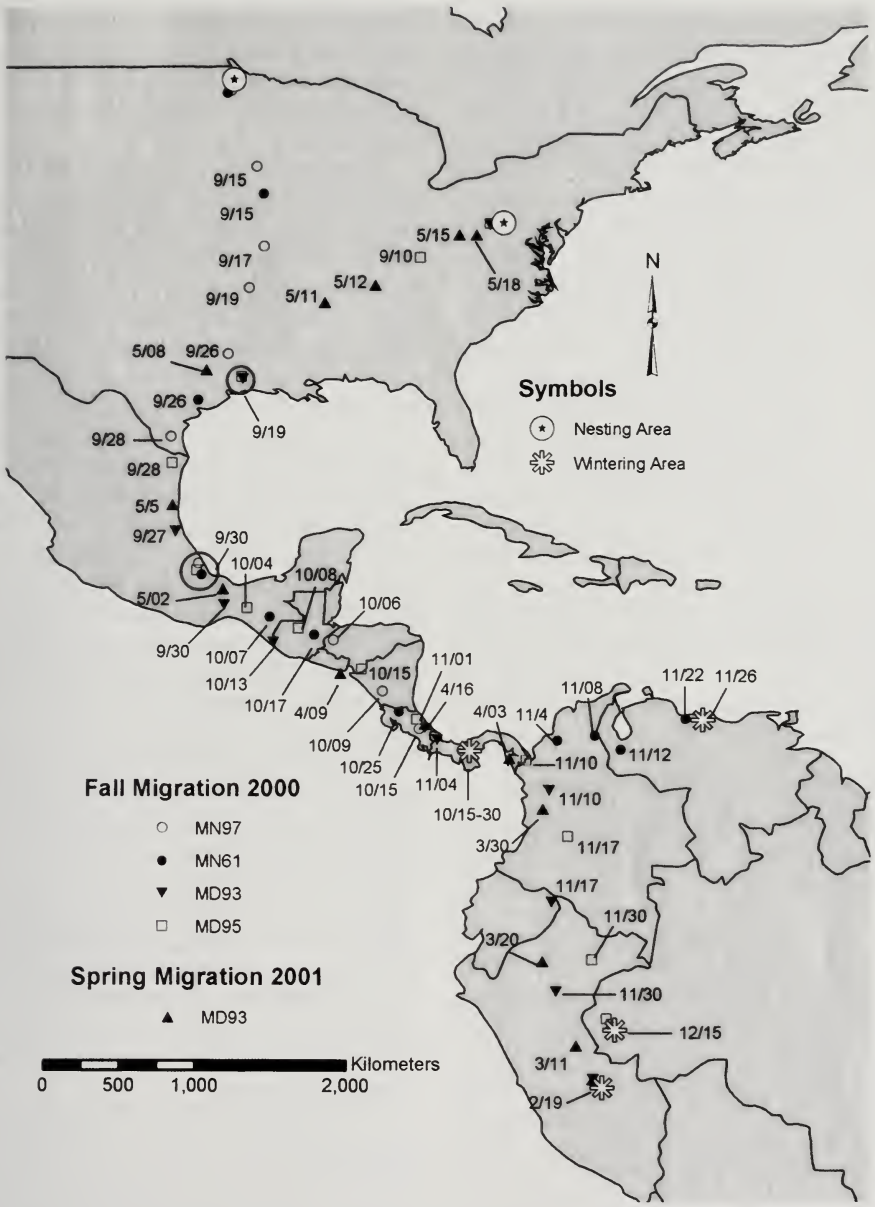

FIG. 1. Broad-winged Hawks nesting in Minnesota and Maryland migrated to wintering grounds in Central and South America. Data were collected by satellite telemetry.

longitude, time and date of transmission, and location error. We analyzed and displayed location data using ArcView ver. 3.2 Geographic Information System (GIS) software (Environmental Systems Research Institute 1992).

We defined the onset of fall and spring migration as the date of first locations after which all subsequent locations occurred at least as far away from the nesting area or wintering area (Fuller et al. 1998). We defined the end of migration as the date after which all subsequent points were localized (nondirectional movements) for the wintering areas and 2001 nesting areas (Fuller et al. 1998). If an activity sensor indicated that a PTT was no longer moving, we presumed that the bird had

died or the PTT had dropped off. To map migration pathways we used a single, high quality (≤1,000 m error) representative location estimate per transmission cycle. For most cycles we used the single highest quality location (Fuller et al. 1998). We visually inspected location estimates using the GIS to remove outliers in the data (Fuller et al. 1998).

We calculated distance traveled by summing the lengths of segments between consecutive representative locations, beginning with the first migration location away from the nesting area and ending with the first wintering (after fall migration) or nesting area (after spring location) location for each hawk. We calculated migration time in days by taking the difference of the estimated departure and arrival date during both fall and spring migration. We calculated migration rates (km/day) by dividing the distance traveled during fall or spring migration by the migration time. We determined wintering areas using the Minimum Convex Polygon (MCP) home range estimator function of the animal movement extension in ArcView 3.2 (Hooge and Eichenlaub 2000).

RESULTS AND DISCUSSION

The four radio-tagged hawks left their nesting areas from about 10–15 September 2000. The fifth hawk, MN88, left her nesting area on 13 September 2000, but we did not receive another transmission until she returned to the same area in spring 2001.

Movements of the four hawks we tracked are presented in Fig. 1. The two Maryland birds moved to Louisiana and the two Minnesota birds migrated through central Iowa, Missouri, and Arkansas. The paths of all four hawks converged in eastern Texas, after which they moved along the Gulf Coast of Texas and Mexico, and then along an inland course through Central America. Bird MN97 ceased her migration and wintered in Panama. The other three hawks moved through Columbia. From Columbia bird MN61 moved to Venezuela where she wintered. Birds MD93 and MD95 continued south through Colombia and past the equator; MD93 wintered in southern Peru and MD95 wintered in southwestern Brazil.

Mean fall migration distance was about 7,000 km (5,625, 6,925, 7,770, and 7,672 km for birds MN97, MN61, MD93, and MD95, respectively), covering 43° of latitude. Mean fall migration time was about 70 days (45, 72, and 90 days for birds MN97, MN61, and MD95, respectively) and mean fall migration rate was about 100 km/day (125, 96, and 85 km/day for birds MN97, MN61, and MD95, respectively).

The wintering areas for all four hawks were in Panama, northern Venezuela, southwestern Brazil, and southern Peru, between 08° 25′ N, 80° 54′ W and 11° 00′ S, 67° 07′ W. Three of the hawks arrived on their wintering areas from about 15 October through 15 December, 2000. The winter area range was 4.3, 2.6, and 1.0 km^2 for birds MN97, MN61, and MD95, respectively.

Three hawks departed from their wintering areas from about 4–29 March 2001, with arrival on the nesting areas about 26 April (bird MN88) and 22 May (bird MD93). Due to radio failures, distance and complete timing for spring migration is available for only one bird (MD93), which had a travel distance of 7,868 km, migration time of 74 days, and a migration rate of 105 km/day. As with bird MN88, bird MD93 returned to the same nesting area used the previous year.

All four hawks tracked during migration followed previously described migration routes (Goodrich et al. 1996) through North America. Details of Broad-winged Hawk migration south of the U.S.-Mexican border are not well documented, but the hawks we tracked did pass over migration count sites in Veracruz, Mexico, and in Panama, and followed the same path described by Smith (1980) through Central America. The few data points we were able to obtain during spring preclude any detailed conclusions about these routes.

All five tracked hawks left their nesting areas within the time period expected, based on published records of Broad-winged Hawk departures (Bednarz et al. 1990). The four hawks tracked during migration crossed Veracruz from 27–30 September 2000, coinciding with the peak Broad-winged Hawk counts there that year (19 September through 5 October; E. R. Inzunza pers. comm.).

Maryland and Minnesota represent the eastern and western portions of the Broad-winged Hawk's breeding range. The similarity in timing and routes taken south of Texas by both the Minnesota and Maryland birds (in agreement with observational and banding data), coupled with similarities in fall migration paths taken by Swainson's Hawks (Fuller et

al. 1998), Ospreys (Martell et al. 2001), and Turkey Vultures (*Cathartes aura*; Smith 1980), have potential conservation implications. These data highlight the importance of the relatively narrow flight path used during a short period of time by all of these species.

Winter area range sizes calculated for three of the hawks were based on 7–11 locations. However, for Northern Bobwhites (*Colinus virginianus*), the MCP home range estimator requires a sample size of >30 locations during a season (10 weeks) for an accurate home range estimation (Haines 2003). While the small sample of locations can give grossly inaccurate home range size estimates (Seaman et al. 1999), the lack of published data on this important aspect of the species biology (Goodrich et al. 1996) compels us to report it, albeit cautiously. While our data suggest that Broad-winged Hawks do not wander during winter and that home range size is constant, more reliable estimations of Broad-winged Hawk winter area range size are needed. Also, more investigation is needed to determine whether the more southerly wintering areas used by the Maryland birds relative to the Minnesota birds indicate winter segregation of hawks nesting in different regions, or whether this was an artifact of small sample size.

This study was the first to track Broad-winged Hawks using satellite telemetry. More extensive radio-tracking studies would aid in understanding the ecology of Neotropical migrants, including migration routes and key wintering areas. This information is essential for developing effective conservation strategies.

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BODY MOLT OF MALE LONG-TAILED DUCKS IN THE NEAR-SHORE WATERS OF THE NORTH SLOPE, ALASKA

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ABSTRACT.—We examined the timing and intensity of body molt in relation to stage of remige growth for postbreeding adult male Long-tailed Ducks (*Clangula hyemalis*) off the coast of northern Alaska. During this period, remige and rectrix feathers are molted simultaneously with body feathers during the prebasic molt, which results in a period of increased energetic and nutritional demands. We collected birds from late July through mid-August and recorded intensity of molt in eight regions: head and neck, back and rump, greater coverts, lesser coverts, flank and sides, breast, belly, and tail. Using nonlinear regression, we estimated the peak intensity and variation for each region in relation to ninth primary length. We found little evidence of molt in the head and neck region. The greater and lesser coverts, and back and rump reached peak molt intensities earliest and were followed by tail, breast, and belly. Molt intensity in the flank and side region was highly variable and indicated a more prolonged molting pattern in relation to other regions. While body molt occurs simultaneously with wing molt, we found that molt among regions occurred in a staggered pattern. Long-tailed Ducks may employ this staggered molting pattern to minimize the energetic and nutritional requirements of molt. *Received 16 July 2002, accepted 22 February 2003.*

Each year during July and August adult male Long-tailed Ducks (*Clangula hyemalis*) migrate in large numbers to the near-shore waters of the North Slope of Alaska (Johnson and Gazey 1992). The shallow lagoons of the region range from 2–3 m in depth and are protected by barrier islands that shelter the lagoon system from high winds and ice flow. During this period, Long-tailed Ducks undergo the prebasic molt (Humphrey and Parkes 1959).

Whereas the molting regimes of most species of waterfowl consist of one or two molting cycles per year (i.e., pre-alternate and prebasic), Long-tailed Ducks are unique in that they carry out an additional third, supplemental molt (Salomonsen 1949, Humphrey and Parkes 1959, and Palmer 1976). The supplemental molt occurs from approximately September through mid-October, between the prebasic and pre-alternate molts, and involves replacement of the head, neck, and scapular regions (Palmer 1976). Subsequently, pre-alternate molt occurs gradually from some time in September through November or December. This molt involves the replacement of all feathering except the tail, wing, and posterior underparts of the bird (Palmer 1976). Prebasic molt occurs in two periods. During spring (commonly April; Palmer 1976), areas including the head down to the breast and much of the mantle are molted. Prebasic molt resumes in late summer (July) and continues into fall when male Long-tailed Ducks molt the remaining body regions as well as remiges. During this molt Long-tailed Ducks are flightless for approximately 3–4 weeks (Palmer 1976).

Molt can be a useful indicator of the physiological status, habitat requirements, and probable fitness of migratory waterfowl (Lovvorn and Barzen 1988). Understanding the timing of prebasic molt is important since it occurs with the wing molt, a period that leaves waterfowl vulnerable to disturbance and predation. During this period birds may lose as much as 25% of their total body mass (Chilgren 1977, King 1980). Nutrient demands increase for the synthesis of new feathers, increased amino acid metabolism, increased cardiovascular activity, daily protein requirements, increased production of red blood cells, and augmented bone formation (Murphy and King 1992). Birds can cope with the added costs of molt by increasing foraging effort, reducing other nutrient costly activities, catabolizing stored nutrients, or a combination of the three (Ankney 1979, Murphy and King 1982). Catabolized reserves often play an important role in supplying the necessary nutri-

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ents to carry out feather replacement (Hanson 1962, Howell 2002, but see Ankney 1979). Therefore, characterizing the body molt as it relates to remige growth provides a composite view of the timing and intensity of molt that could serve as a potential baseline from which to measure the effects of physiological or environmental pressures on the population. Our primary assumption was that while the precise timing of molt may vary among years and individuals, the relative timing of feather molt is a good indicator of the physiological status and capability of individuals to meet the nutritional demands of the process. Our objective was to describe the timing and intensity of body molt in relation to the stage of remige molt as it occurs in adult male Long-tailed Ducks.

METHODS

We conducted this study at two sites in near-shore waters of the Beaufort Sea on the northern coast of Alaska, Simpson Lagoon (70° 32′ N, 149° 26′ W) and an unnamed lagoon formed by the Maguire Islands and Flaxman Island (70° 12′ N, 146° 19′ W). During the summers of 1999 and 2000 we attempted to obtain comparable samples of birds from each site representing all stages of the wing molt from just following remige loss through feather growth and re-attainment of flight. We obtained specimens by euthanizing birds captured during banding operations or by shooting after significant numbers of flightless birds had been observed in the area in accordance with Auburn Univ. Animal Care and Use Committee guidelines. We shot individuals from flocks after first establishing their inability to fly by observations from blinds or by approaching them with small boats. We selected individuals for euthanasia during banding drives based on the length of the ninth primary in order to ensure broad distribution of molt stages and dates. Specimens then were frozen and transported to Auburn Univ. for laboratory analysis.

We determined stage of wing molt by measuring the length of the ninth primary from the tip of the feather to its insertion on the proximal side of the feather. To measure the intensity of body molt, we assigned feather tracts into eight regions: (1) head and neck (crown, facial, chin/throat, and neck), (2) back and rump (upper and lower back, scapulars, rump), (3) breast (chest), (4) belly; (5) greater coverts, (6) lesser coverts, (7) side (flank and side), and (8) rectrices, based on Billard and Humphrey (1972). We sampled each region four times by estimating the proportion of blood quills and missing feathers along a 2.54-cm dissecting probe inserted between feathers at random locations. We defined a blood quill as any growing feather containing blue color within the shaft or any feather with feather sheath present at or above the skin surface. We categorized molt intensity into five levels based on the estimated portion of blood quills and missing feathers in each sample: 0 (0%), 1 (1–25%), 2 (26–50%), 3 (51–75%), and 4 (>75%) based on Taylor (1995), and recorded the mean score for each region.

Analysis.—We were interested in estimating the intensity and duration of molt for each feather tract with respect to the stage of wing molt. We sought to do so using a model that would adequately describe the distribution of molt intensity scores with respect to remige length using biologically interpretable and estimable parameters. Although linear, polynomial, and other nonlinear models could adequately describe the shape of the sample distribution, they failed to incorporate meaningful information about similar biological phenomena that occur during finite time periods. Thus, we selected a model that would estimate the mean maximum molt intensity, the timing of maximum molt intensity, and variability in molt intensity over time. We used nonlinear regression (Sigmaplot 2001 ver. 7.0; SPSS, Inc. 2001) to fit the Gaussian three-parameter model,

$$y = a \exp\left[-0.5\left(\frac{x - x_0}{b}\right)^2\right],$$

where the estimated parameter a corresponds to the function maxima, b determines the width of the bell curve, x is the independent variable, x_0 is the estimated value of the independent variable at the corresponding function maxima, and y is the dependent variable. Thus, for a given feather tract and individual, y and x are the observed molt score and length of the ninth primary (i.e., molt stage). It follows then that the population parameters estimated for each feather tract are, a = mean

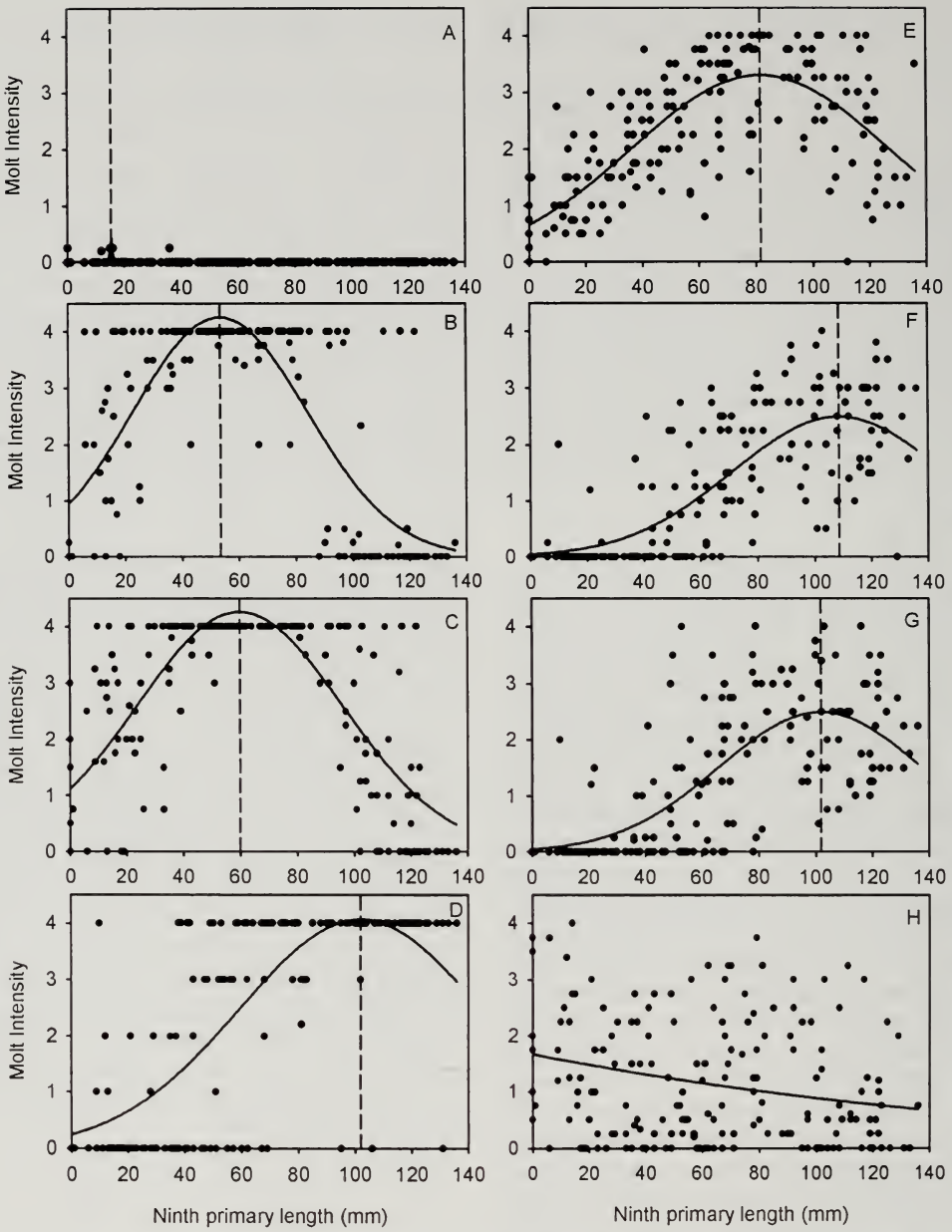

FIG. 1. Distributions of molt intensity scores for adult male Long-tailed Ducks by body region: (A) Head and neck, (B) lesser coverts, (C) greater coverts, (D) tail, (E) back and rump, (F) belly, (G) breast, and (H) flank and side. Score distributions indicate that the timing of molt varied with respect to stage of remige regrowth. Solid lines are mean-fitted distributions, and dotted lines indicate the estimated stage of wing molt (i.e., ninth primary length) corresponding to peak molt intensity.

peak molt intensity, b = variation in molt intensity with respect to molt stage, and x_0 = length of ninth primary at which molt intensity peaks. A high degree of synchrony in molt among individuals resulted in good model fit as indicated by a large R^2. Large variability in timing of peak molt intensity with respect to molt stage was indicated by a relatively large b. Thus, a small R^2 in concert with a large value for b suggested a low de-

TABLE 1. Intensity of body molt of adult male Long-tailed Ducks using Beaufort Sea lagoons during 1999–2000 varied with respect to the stage of remige molt (length of ninth primary in mm) as indicated by parameter estimates (a, b, x_0) that describe a bell-shaped curves (three-parameter Gaussian models) of molt intensity. Large variation in b and poor model fit (low R^2) suggests that molt on flanks and sides were not synchronous with remige molt.

Region	Maximum intensity (a) Estimate (SE)	Variance in intensity (b) Estimate (SE)	Remige molt stage at peak intensity (x_0) Estimate (SE)	R^2
Head and Neck	0.43 (1.32)	0.38 (0.85)	15.40 (0.47)	0.30
Back and Rump	3.30 (0.10)	45.53 (2.35)	81.59 (1.89)	0.53
Breast	2.49 (0.13)	35.73 (3.40)	101.70 (3.35)	0.52
Flank and Side	8.37 (119.14)	306.61 (1374.08)	−550.31 (5218.59)	0.06
Greater Coverts	4.25 (0.12)	36.44 (1.43)	59.81 (1.30)	0.63
Lesser Coverts	4.25 (0.15)	30.74 (1.36)	53.35 (1.30)	0.65
Tail	4.06 (0.15)	42.84 (3.42)	101.94 (3.49)	0.60
Belly	2.49 (0.11)	37.63 (3.55)	108.52 (3.96)	0.59

gree of synchrony in feather molt at the population level.

RESULTS

We collected specimens (n = 187) from 28 July to 14 August 1999, and from 21 July to 10 August in 2000. Long-tailed Ducks molted each body region during our study except head and neck (Fig. 1, Table 1). Although we found evidence of feather regrowth, only six males (3%) showed any degree of molt in the head and neck (Fig. 1A).

During our study, molt intensity achieved the highest levels in the lesser coverts, greater coverts, tail, and back and rump regions. Nonlinear models explained over 60% of the variation in molt scores for lesser and greater coverts. Lesser coverts appeared to reach the highest molt intensity slightly earlier than greater coverts (Fig. 1B and 1C). The back and rump region also reached highest molt intensity when remiges were slightly more than half of their full length (Fig. 1E). Rectrices were the next feathers to reach peak molt intensity (Fig. 1D). Both the lesser and greater coverts appeared to complete the process of molt before remige regrowth was complete, while the back and rump regions were nearly completed during the same time period. Molt of rectrices appeared to have continued into the latter stages of remige regrowth.

Our models explained nearly 60% of the variation in molt scores for the breast region and over 50% for the belly region (Table 1). We found that the breast and belly regions started molt later than the greater and lesser coverts, rectrices, and back and rump regions and attained maximum molt intensity during the latter half of molt. The breast region attained maximum intensity slightly ahead of the belly region (Fig. 1G and 1F). However, the figures indicate that the latter stages of feather growth for the breast and belly regions did not occur within our study period and probably continued until and perhaps beyond full remige regrowth.

Molt in the side and flank region occurred throughout our study (Fig. 1H). Values for molt intensity in this region also were highly variable as indicated by the value of b for this feather tract (Table 1).

DISCUSSION

All feather tracts, except the head and neck and the flank and side regions, increased in molt intensity as wing molt progressed. Our research substantiated Palmer's (1976) characterization that molt occurs in the head and neck region prior to all other feather tracts during the prebasic molt. Molt in the flank and side region appear to be more variable throughout the wing molt and the lack of a discernable peak probably indicates a slower rate of molt in these areas. Both the greater and lesser coverts and the back and rump regions began molting concurrent with the loss of remiges and were regrown by the time remige regrowth was complete.

Long-tailed Ducks may reduce the nutritional demands of molt by staggering the molt of various feather regions over time or by undergoing molt during periods when molt does

not overlap with other nutrient costly activities such as migration (Heitmeyer 1987). Our data indicate that greater and lesser coverts and back and rump regions likely completed molt prior to additional postbreeding movements, which may reduce costs associated with the initiation of the supplemental molt as it begins in September (Palmer 1976). However, King and Murphy (1985) advised that nutritional status should be considered in the context of the life history of a species with regard to nutritional requirements and accessibility, as well as the repertoire of adjustments available to avert or minimize discrepancies between the two. Also, Lovvorn and Barzen (1988) cautioned against the interpretation of molt patterns in terms of staggered costs and found that timing of molt was associated with a photoperiodic response for Canvasbacks (*Aythya valisineria*). Leafloor and Ankney (1991) also suggested that among unsuccessful nesting female Mallards (*Anas platyrhynchos*) social environment appears to influence the timing of molt. For Long-tailed Ducks molting in the cold waters of the Beaufort Sea, a less synchronous pattern of body molt also may lessen the thermal costs associated with reduced insulatory qualities of plumage.

Also, completion of the covert molt prior to full remige regrowth may suggest an adaptive strategy to minimize the flightless period. Many species of waterfowl regain flight before remige regrowth is complete (Hohman et al. 1992). Brown and Saunders (1998) showed that body mass dynamics and wing surface area played a significant role in enabling Blue-winged Teal (*Anas discors*) to re-attain flight capability before remige growth was complete. However, smoothness and shape of the wing also are important in reducing wing drag and maximizing lift (Pennycuick 1989). We suggest that while the overall timing of molt in Long-tailed Ducks may be controlled by ultimate factors such as photoperiod, the sequence of molt among specific feather tracts, specifically the molt of wing coverts, is timed to reduce the period of flightlessness. Further, the staggered timing of molt among feather tracts may serve to spread the nutritional demands of feather growth and reduce the energetic costs associated with thermoregulation in cold water environments.

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DIURNAL AND NOCTURNAL BEHAVIOR OF BREEDING AMERICAN AVOCETS

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ABSTRACT.—We studied nocturnal and diurnal behavior of breeding American Avocets (*Recurvirostra americana*) at the Jay Dow, Sr. Wetlands in the northwestern Great Basin, USA. Seven-day observation periods were centered on two full moons when ambient light was maximal and auxiliary lighting unnecessary. We recorded avocet density, habitat use, interbird distances, and behavior three times daily (beginning at 07:00, 15:00, 23:00 PST) for 14 days. We calculated the mean proportion of individuals within flocks engaged in four behavior classes (foraging, copulating, agonistic, other). Foraging birds were further subdivided by technique (pecking, dunking, scything). Avocets copulated with similar frequencies during the morning, afternoon, and night. Avocets were more aggressive and closely spaced at night than during day. The full repertoire of behaviors seen during daylight also occurred at night, though frequencies of particular behaviors, flock location, and interbird distances varied among morning, afternoon, and nighttime observations. The role of nocturnal reproductive behavior should be assessed in species generally perceived as being diurnal. *Received 12 January 2003, accepted 20 March 2003.*

Nocturnal foraging throughout the annual cycle is common among coastal shorebirds in North and South America, Africa, and Europe (Goss-Custard 1969, McNeil and Robert 1988, Zwarts et al. 1990, McNeil 1991, Evans and Harris 1994, Staine and Burger 1994), yet there is relatively little understanding of the latitudinal and seasonal variation in nocturnal behavior within and among shorebird species. Researchers have proposed that tactile foragers should be relatively less affected by darkness than visual foragers (Vader 1964, Goss-Custard 1969, Evans 1976, Dugan 1981), yet plovers (Charadriidae) are primarily visual foragers that commonly forage at night (Pienkowski 1983). The relatively large eye in relation to head size of plovers may enhance visual detection of prey (Evans 1976), yet several smaller-eyed sandpipers (Scolopacidae) also forage visually at night, including Common Redshanks (*Tringa totanus*; Goss-Custard 1969), Semipalmated Sandpipers (*Calidris pusilla*; Evans 1979), and Whimbrels (*Numenius phaeopus*; McNeil and Rompré 1995). Nocturnal bird species are morphologically and physiologically adapted to nocturnal activity as their eyes contain a higher proportion of rods in the retina compared to diurnal species, and retinal sensitivity is higher among birds that forage visually at night compared to those that use tactile techniques (Tansley and Erichsen 1985; Rojas De Azuaje et al. 1993; Rojas et al. 1999a, 1999b; McNeil et al. 1999).

Although several studies have examined nocturnal foraging at coastal locations, there are few studies of shorebird nocturnal behavior on the breeding grounds and at inland locations. During the breeding season, Red-wattled Lapwings (*Vanellus indicus*) and Stone-curlews (*Burhinus oedicnemus*) are vocal primarily at night (Bannerman 1959), and some species display or call from dusk into the night (*Scolopax* spp.: Sheldon 1961, Krohn 1971, Stribling and Doerr 1985; *Gallinago* spp.: Lemnell 1978). Breeding Common Ringed Plovers (*Charadrius hiaticula*), and Piping Plovers (*C. melodus*) forage at night (Pienkowski 1983, Staine and Burger 1994), and the role each sex plays in nocturnal incubation also has been examined for several species (Laven 1940, Mundahl 1982, Warriner et al. 1986, Staine and Burger 1994, Thibault and McNeil 1995a, Warnock and Oring 1996). American (*Recurvirostra americana*) and Pied avocets (*R. avosetta*) forage diurnally and nocturnally throughout the annual cycle (Evans and Harris 1994, Dodd and Colwell 1996, Hötker 1999, Johnson et al. 2002), and

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TABLE 1. Akaike Information Criteria (AIC) for candidate models used to examine variation in American Avocet behavior during the daily cycle at Jay Dow, Sr. Wetlands, Lassen County, California, 2001.

Model[a]	Number of parameters	ΔAIC[b]	AIC weight[c]
Overall behavior			
{T, L, D, W, L × D}	5	0.0	0.865
{T, L, D, W, T × L, T × D, L × D}	7	3.7	0.135
{T, FS, L, D, EL, W, S, I, dist, inter}	23	35.1	<0.001
Habitat use			
{T, L, FS, A, T × L}	5	0.0	0.932
{T, FS, L, F, A, T × FS, T × L}	8	5.9	0.050
{T, FS, L, F, A, 5, T × FS, T × L, FS × L}	9	7.8	0.019
Interbird distance			
{T, FS, L, D, EL, T × L, L × D}	7	0.0	0.999
{T, FS, L, D, EL, inter}	15	15.2	0.001
{T, FS, L, D, EL, M, A, C, F, W, S, I, inter}	22	29.0	<0.001
Foraging technique			
{T, FS, L, D, EL, W, 1, T × EL, L × D}	9	0.0	0.873
{T, FS, L, D, EL, W, 1, T × EL, L × D, T × D, FS × L}	11	3.9	0.127
{T, FS, L, D, EL, W, 1, inter}	17	15.5	<0.001

[a] T = treatment (morning = 07:00, afternoon = 13:00, night = 23:00), FS = flock size, L = location, D = date, EL = early/late season, F = proportion foraging, M = proportion self maintenance, C = proportion copulating, A = proportion agonistic, W = proportion in open water, S = proportion on shore, I = proportion on islands, 1 = proportion of birds <1 m apart, 5 = proportion of birds 1–5 m apart, dist = all interbird distance classes (<1, 1–5, 6–10, 11–20, >20 m), inter = all two-way interactions.

[b] ΔAIC is the rank of each model by rescaling the model with a minimum AIC value to zero ($\Delta AIC = AIC_i - AIC_{min}$).

[c] AIC weights are the likelihood of the model given the data (Akaike weights).

several shorebird species, including the American Avocet, copulate at night (Johnson et al. 2002).

Knowledge of nocturnal behavior is essential for understanding both ecology and energetics, yet current understanding of shorebird nocturnal behavior is limited. Shorebird habitat use and foraging technique varies during the daily cycle (Rompré and McNeil 1995, Robert et al. 1989). Nocturnality also appears to affect energy balance (Pienkowski 1983) and, potentially, reproductive strategy (Johnson et al. 2002). Recent technological advances in night vision equipment facilitate the study of nocturnal behavior, permitting a more thorough approach to behavioral ecology and allowing more accurate assessment of energy budgets, space use, and social interactions. The aim of this study was to describe the extent of nocturnality among American Avocets breeding at an inland location.

METHODS

Study area.—We studied American Avocet behavior at the Jay Dow, Sr. Wetlands (JDW; 40° 07′ N, 120° 14′ W, elevation 1,220 m). JDW is a 540-ha constructed wetland containing 16 bodies of water at the southern end of Honey Lake, Lassen County, California. JDW includes a seep draining to Honey Lake, a natural playa lake, and 14 constructed ponds. With the exception of the seep, water was maintained at a constant level from March to July. Honey Lake Basin (23,000 ha) is characterized by agricultural production and by Great Basin desert scrub vegetation on gently sloping to nearly level alluvial fans, floodplain, and basin floor. Common vegetation at JDW included sagebrush (*Artemisia tridentata*), saltbrush (*Atriplex spinosa*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), saltgrass (*Distichlis spicata*), rush (*Juncus* spp.), and cattail (*Typha latifolia*). Avocets arrive at JDW during late March and initiate clutches from the end of April through the beginning of June (Robinson and Oring 1997).

Observations.—During 2001, we centered 7-day observation periods on two full moons (3–10 May and 2–8 June) when ambient light was maximal and auxiliary lighting unnecessary. We used a hand-held generation III night

TABLE 2. Multivariate analysis of variance for time of day (07:00, 13:00, 23:00) and covariate effects on American Avocet behavior at Jay Dow, Sr. Wetlands, Lassen County, California, 2001.

Factor	Degrees of freedom		Wilk's lambda	*F*	*P*
	Numerator	Denominator			
Overall behavior					
Time of day	8	210.00	0.278	23.52	<0.001
Date	4	105.00	0.679	12.40	<0.001
Location	28	380.01	0.434	3.54	<0.001
Proportion birds in open water	4	105.00	0.770	7.84	<0.001
Date × location	24	367.51	0.663	1.92	0.007
Habitat use					
Time of day	6	200.00	0.691	6.77	<0.001
Location	21	287.70	0.199	10.37	<0.001
Flock size	3	100.00	0.934	1.62	0.189
Proportion birds agonistic	3	100.00	0.954	1.61	0.192
Time of day × location	36	296.19	0.568	1.73	0.008
Interbird distance					
Time of day	10	182.00	0.328	13.59	<0.001
Date	5	91.00	0.719	7.12	<0.001
Month	5	91.00	0.744	6.25	<0.001
Location	35	385.23	0.630	1.28	0.139
Flock size	5	91.00	0.728	6.79	<0.001
Location × time of day	60	429.90	0.644	0.70	0.952
Location × date	30	366.00	0.570	1.84	0.005
Foraging technique					
Time of day	6	202.00	0.749	5.24	<0.001
Date	3	101.00	0.799	8.47	<0.001
Month	3	101.00	0.789	8.98	<0.001
Location	21	290.57	0.430	4.73	<0.001
Flock size	3	101.00	0.891	4.14	0.008
Proportion birds in open water	3	101.00	0.645	18.54	<0.001
Proportion birds <1 m apart	3	101.00	0.892	4.10	0.009
Time of day × month	6	202.00	0.865	2.54	0.022
Location × date	18	286.16	0.717	1.98	0.011

vision scope with a 100-mm zoom lens (NiteMate NAV-3, Litton) to observe avocet behavior at night. We established 43 observation points that enabled total coverage of JDW during diurnal and nocturnal surveys. We recorded avocet density, habitat use, and behavior three times daily (morning, afternoon, and night: 07:00, 15:00, and 23:00 PST, respectively) for 14 days at each observation point. We recorded avocet density for each pond and the entire study site. We recorded the distance from each individual to the nearest next individual as one of five interbird distance classes (<1 m, 1–5 m, 6–10 m, 11–20 m, >20 m), and we categorized occupied habitats as shoreline, open water, or island. We categorized behavior as foraging, copulating, agonistic, or other. Agonistic behavior refers to intraspecific encounters, and behavior class "other" included self maintenance, nest building, and incubation. We further subdivided foraging birds by technique (pecking, dunking, scything). Foraging classes corresponded to the visual (pecking) and tactile (dabbling scythe and multiple scythe) foraging techniques described by Hamilton (1975). After we completed each survey of JDW (approximately 1 h), we returned to the three locations containing the largest avocet flocks and scanned flocks, recording each bird's behavior. We scanned each flock five times with ≥3 min between successive samples. Time required per scan sample (1–3 min) varied with flock size. The five scans represented subsamples of each flock, which we used as our experimental unit (mean proportion of total number of av-

ocets present at JDW for which individual behavior was recorded after each census was 0.74 ± 0.07 SD, n = 42 censuses, n = 126 flocks).

Analysis.—From each set of scans, we calculated the mean proportion of individuals within each flock engaged in the four behavior classes, as well as the proportion of foraging birds utilizing each foraging technique. We also calculated the proportion of birds in each habitat, and the proportion of birds in each of five interbird distance classes. These methods produced four multidimensional response vectors for the behavior of each flock. The response vectors (behavior, foraging technique, habitat use, interbird distance) served as independent data points for analysis. Because percentages within vectors summed to 100 and were thus correlated, it was necessary to use multivariate analysis techniques. We arcsine transformed data and set alpha = 0.05 *a priori,* then tested for behavioral variation during the daily cycle using a multivariate analysis of covariance model (MANCOVA) for each response vector, with time of day (morning, afternoon, night) as the main effect and month (May, June), date (day one through seven during May and June sampling periods), location (pond), and flock size as covariates (Seber 1984, Johnson and Wichern 1988). Behavioral responses not modeled by the response vector also were included as covariates in each model. We compared potential models for each behavioral response beginning with the saturated two-way interactive model using information-theoretic methods to direct model selection (Burnham and Anderson 1998). For each model we calculated Akaike information criteria (AIC), which were used to compare candidate models to achieve the most parsimonious model that accurately represented the data (Burnham and Anderson 1998, Anderson et al. 2000).

We used three-way ANOVA to examine avocet density at ponds during the daily cycle (morning, afternoon, night) and throughout the study (May, June). We used SAS macro FXQLQLQL (Fernandez 1999) to check normality and equal variance assumptions of ANOVA and examined student residuals for the presence of significant outliers and influential observations. Data differed significantly from normality and variances were not equally distributed. When we performed Huber's iterative robust ANOVA to reduce the impact of highly influential observations, the data assumed a normal distribution (D'Agostino-Pearson Omnibus P = 0.62; Huber 1981). We used Tukey's test for comparison of all means, and we report nontransformed values.

RESULTS

Avocet behavior varied within the daily cycle, and among days, locations, and months. The mean number of avocets was similar at all times of day (morning: 148 ± 14 SE, afternoon: 145 ± 12 SE, night: 157 ± 8 SE; P = 0.92), but more avocets were present early in the breeding season than later (May: 170 ± 6 SE, June: 130 ± 10 SE; P = 0.015).

Behavior.—Behavior (foraging, copulating, agonistic, other) varied as a function of time of day, date, proportion of birds in open water habitat, and location (Tables 1, 2). There also was a significant interaction between date and location (Tables 1, 2). We found no significant difference in the proportion of avocets copulating or foraging throughout the day (Table 3). However, birds were five times more agonistic at night compared to morning and afternoon (Table 3), and birds engaged in other behavior less at night than during morning and afternoon (Table 3).

Foraging technique.—Foraging technique varied as a function of time of day, flock size, location, date, month (Table 4), open water habitat, and proportion of birds < 1m from another avocet (Tables 1, 2). There also was an interaction between time of day and month and between location and date (Tables 1, 2). Avocets foraged by pecking more in the morning compared to afternoon and night (Table 3). The proportion of birds dunking increased from morning to afternoon and again from afternoon to night (Table 3), and higher proportions of avocets foraged by dunking early in the breeding season compared to later (Table 4). Avocets scythed less at night than during day (Table 3), and lower proportions of avocets used the scythe technique to forage early in the breeding season than later (Table 4).

Habitat use.—Habitat use by avocets varied as a function of time of day and location, and there was a significant interaction between these two variables (Tables 1, 2). Avocets fre-

TABLE 3. Mean (± SE) proportion of American Avocets conducting various behaviors in different habitats during three daily sampling periods (morning = 07:00, afternoon = 13:00, night = 23:00) in early (May; n = 21 flocks) and late (June; n = 21 flocks) breeding season and combined (May–June; n = 42) at Jay Dow, Sr. Wetlands, Lassen County, California, 2001. Different superscripts within a row denotes statistically different means (Tukey's test, $P < 0.05$).

	Morning			Afternoon	
	May	June	May–June	May	June
Behavior					
Agonistic	0.019 ± 0.007	0.026 ± 0.009	0.023 ± 0.006[A]	0.040 ± 0.009	0.033 ± 0.008
Copulate	0.017 ± 0.005	0.005 ± 0.002	0.011 ± 0.003[A]	0.027 ± 0.005	0.002 ± 0.001
Other	0.449 ± 0.060	0.350 ± 0.033	0.400 ± 0.035[A]	0.421 ± 0.042	0.425 ± 0.035
Foraging	0.515 ± 0.057	0.620 ± 0.034	0.567 ± 0.034[A]	0.512 ± 0.038	0.540 ± 0.033
Dunking	0.591 ± 0.075	0.466 ± 0.063	0.529 ± 0.049[A]	0.777 ± 0.056	0.446 ± 0.068
Pecking	0.395 ± 0.077	0.213 ± 0.047	0.304 ± 0.047[A]	0.186 ± 0.053	0.231 ± 0.040
Scything	0.014 ± 0.005	0.321 ± 0.058	0.168 ± 0.037[A]	0.037 ± 0.027	0.323 ± 0.063
Habitat					
Water	0.510 ± 0.081	0.847 ± 0.038	0.679 ± 0.051[A]	0.705 ± 0.054	0.733 ± 0.038
Island	0.261 ± 0.073	0.042 ± 0.020	0.151 ± 0.041[A]	0.130 ± 0.050	0.039 ± 0.019
Shore	0.229 ± 0.053	0.111 ± 0.028	0.170 ± 0.031[A]	0.164 ± 0.027	0.227 ± 0.033
Interbird distance					
<1 m	0.160 ± 0.032	0.062 ± 0.016	0.111 ± 0.020[A]	0.222 ± 0.032	0.113 ± 0.024
1–5 m	0.230 ± 0.029	0.180 ± 0.025	0.205 ± 0.019[A]	0.280 ± 0.021	0.243 ± 0.027
6–10 m	0.209 ± 0.024	0.221 ± 0.024	0.215 ± 0.017[A]	0.175 ± 0.025	0.184 ± 0.024
11–20 m	0.193 ± 0.031	0.380 ± 0.036	0.287 ± 0.028[A]	0.144 ± 0.018	0.292 ± 0.045
>20 m	0.207 ± 0.029	0.157 ± 0.025	0.182 ± 0.019[A]	0.179 ± 0.016	0.169 ± 0.027

quented certain ponds at specific times of the day and some ponds were used predominately during either the early or late portion of the breeding season (Fig. 1; ANOVA: $F_{46,416} = 36.39$, $P < 0.0001$; location $F_{10,416} = 61.65$, $P < 0.0001$; month $F_{1,416} = 13.44$, $P = 0.0003$; time of day $F_{2,416} = 0.49$, $P = 0.61$; time of day × location $F_{20,416} = 0.3.47$, $P < 0.0001$; month × location $F_{10,416} = 17.84$, $P < 0.0001$; month × time of day $F_{2,416} = 9.0$, $P = 0.0001$). Island habitat use decreased from morning through night (Table 3), and a greater proportion of avocets used islands early in the breeding season compared to later (Table 4). Mean proportion of avocets utilizing open water did not differ significantly among the three sampling periods (Table 3), but avocets used open water more often late in the breeding season (Table 4). The proportion of avocets utilizing shoreline habitat did not differ significantly among the three daily sampling periods (Table 3) or between early and late season (Table 4).

Interbird distance.—Interbird distance varied as a function of time of day, flock size, date, and month (Tables 1, 2). There also was an interaction between date and location (Tables 1, 2). Mean proportion of avocets < 1m apart was higher at night than during day (Table 3). Similarly, the proportion of birds 1–5 m apart was higher in the afternoon compared to morning but greatest at night (Table 3). The proportion of birds in all larger interbird distance classes was least at night (Table 3). Mean proportion of avocets < 1m apart was higher early in the season, and a larger proportion of birds were spaced farther apart later in the season (Table 4).

DISCUSSION

All behaviors performed by breeding American Avocets during the day also occurred at night, though frequencies of particular behaviors, flock location, and interbird distances varied among morning, afternoon, and night. Nocturnal social behavior was sufficiently frequent that further study of avocet behavior must consider nocturnal habits. While observations in this study were limited to the week around the full moon, earlier observations at the study site confirm that several shorebird species are socially active at

TABLE 3. Extended.

Afternoon	Night		
May–June	May	June	May–June
0.036 ± 0.006[A]	0.186 ± 0.017	0.210 ± 0.021	0.198 ± 0.014[B]
0.014 ± 0.003[A]	0.025 ± 0.008	0.008 ± 0.003	0.016 ± 0.004[A]
0.423 ± 0.027[A]	0.240 ± 0.028	0.160 ± 0.019	0.200 ± 0.018[B]
0.526 ± 0.025[A]	0.549 ± 0.027	0.623 ± 0.026	0.586 ± 0.019[A]
0.612 ± 0.051[B]	0.816 ± 0.037	0.685 ± 0.055	0.750 ± 0.034[C]
0.209 ± 0.033[B]	0.142 ± 0.032	0.204 ± 0.045	0.173 ± 0.028[B]
0.180 ± 0.041[A]	0.042 ± 0.017	0.111 ± 0.028	0.076 ± 0.017[B]
0.719 ± 0.033[A]	0.776 ± 0.035	0.768 ± 0.027	0.772 ± 0.022[A]
0.085 ± 0.027[B]	0.053 ± 0.016	0.002 ± 0.001	0.027 ± 0.009[C]
0.196 ± 0.022[A]	0.171 ± 0.029	0.231 ± 0.027	0.201 ± 0.020[A]
0.167 ± 0.021[A]	0.438 ± 0.024	0.305 ± 0.023	0.372 ± 0.019[B]
0.261 ± 0.017[B]	0.312 ± 0.017	0.419 ± 0.016	0.365 ± 0.014[C]
0.179 ± 0.017[A]	0.063 ± 0.009	0.138 ± 0.010	0.101 ± 0.009[B]
0.218 ± 0.027[B]	0.086 ± 0.010	0.079 ± 0.015	0.082 ± 0.009[C]
0.174 ± 0.015[A]	0.101 ± 0.012	0.059 ± 0.010	0.080 ± 0.008[B]

night throughout the lunar cycle (Johnson et al. 2002). Further, Pied Avocets are active at night, regardless of lunar illumination (Hötker 1999).

Copulations.—Nocturnal copulation rarely has been reported, but is not necessarily uncommon among shorebirds (Lemnell 1978, Johnson et al. 2002). We found avocets copulating with similar frequency during morning, afternoon, and night, and previous observation at JDW found several shorebird species, including avocets, copulating at night regardless of lunar phase (Johnson et al. 2002). Theory on mating strategy has failed to address the possibility of nocturnal reproductive tactics among most shorebirds (e.g., Oring 1982). Considering that Ring-billed Gull (*Larus delawarensis*) copulations are interrupted less often at night (Hébert and McNeil 1999), and our observation that nocturnal copulations are likely to play substantial roles in avocet reproduction, study of shorebird nocturnality is critical for accurate assessment of reproductive tactics among temperate breeding shorebirds.

Interbird distance and agonistic behavior.—Avocets were more aggressive and more closely spaced at night than during the day, and the mean proportion of agonistic birds was five times higher at night. Avocets apparently increased nocturnal agonistic behavior at the expense of self maintenance or incubation, as the proportion of birds engaged in other behaviors was 50% less at night. Avocets and other shorebirds potentially are better able to reduce incubation duties at night when the risk of desiccation to uncovered eggs due to overheating is minimal (Thibault and McNeil 1995a). Shorebird eggs are robust to cool temperatures, but highly susceptible to extreme heat. Thus, avocets may be more prone to leave the nest at night when ambient temperature is low. Conversely, it is possible that we failed to detect incubating birds during nocturnal observations. However, this is not likely as there was no significant difference in the number of birds observed on the entire wetland during morning, afternoon, and nocturnal surveys.

Avocets also may be tightly spaced at night to reduce the threat of predation. However, nocturnal agonistic encounters generally were

TABLE 4. Mean (± SE) proportion of American Avocets performing various behaviors in different habitats early (May; n = 63 flocks) and late (June; n = 63 flocks) in the breeding season at Jay Dow, Sr. Wetlands, Lassen County, California, 2001. Different superscripts within a row denotes statistically different means (Tukey's test, $P < 0.05$).

	May	June
Behavior		
Agonistic	0.082 ± 0.012^{A}	0.089 ± 0.013^{A}
Copulate	0.023 ± 0.004^{A}	0.005 ± 0.001^{A}
Other	0.370 ± 0.028^{A}	0.312 ± 0.022^{A}
Foraging	0.526 ± 0.024^{A}	0.594 ± 0.018^{A}
Dunking	0.728 ± 0.035^{A}	0.532 ± 0.038^{B}
Pecking	0.241 ± 0.035^{A}	0.216 ± 0.025^{A}
Scything	0.031 ± 0.011^{A}	0.252 ± 0.032^{B}
Habitat use		
Water	0.664 ± 0.037^{A}	0.783 ± 0.021^{B}
Island	0.148 ± 0.031^{A}	0.027 ± 0.009^{B}
Shore	0.188 ± 0.022^{A}	0.190 ± 0.018^{A}
Interbird distance		
<1 m	0.273 ± 0.023^{A}	0.160 ± 0.018^{B}
1–5 m	0.274 ± 0.014^{A}	0.281 ± 0.018^{A}
6–10 m	0.149 ± 0.014^{A}	0.181 ± 0.012^{A}
11–20 m	0.141 ± 0.014^{A}	0.250 ± 0.025^{B}
>20 m	0.163 ± 0.013^{A}	0.128 ± 0.014^{B}

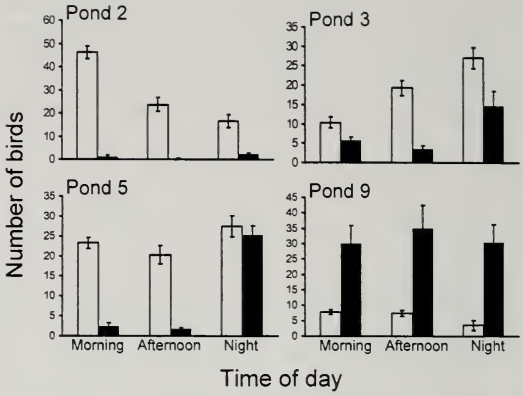

FIG. 1. Variation in mean number of American Avocets at four locations at Jay Dow, Sr. Wetlands, Lassen County, California during morning (07:00), afternoon (15:00), and night (23:00) observations, 2001. White bars represent May observations (n = 7), black bars represent June observations (n = 7), and error bars provide standard error (ANOVA: all locations, n = 11: $F_{46,416} = 36.39$, $P < 0.0001$; location $F_{10,416} = 61.65$, $P < 0.0001$; month $F_{1,416} = 13.44$, $P = 0.0003$; time of day $F_{2,416} = 0.49$, $P = 0.61$; time of day × location $F_{20,416} = 0.3.47$, $P < 0.0001$; month × location $F_{10,416} = 17.84$, $P < 0.0001$; month × time of day $F_{2,416} = 9.0$, $P = 0.0001$).

loud and created a commotion easily detected by predators. Hawk and owl predation is a key factor in shorebird mortality during the nonbreeding season (Page and Whitacre 1975, Townshend 1984, Whitfield 1985, Whitfield et al. 1988); however, the extent of diurnal versus nocturnal raptor predation on shorebirds, especially during the breeding season, has not been thoroughly investigated (Townshend 1984).

Foraging.—The proportion of birds engaged in foraging behavior varied from 0.50–0.60 throughout the daily cycle and the entire season; however, foraging technique was less consistent. Change in prey visibility or availability may account for daily and seasonal variation in foraging technique. A shift to tactile foraging techniques at night may be more efficient for avocets if prey is difficult to detect visually at lower light intensities. Eurasian Oystercatchers (*Haematopus ostralegus*), yellowlegs (*Tringa flavipes*, *T. melanoleuca*), Black-winged Stilts (*Himantopus himantopus*), and Willets (*Catoptrophorus semipalmatus*) showed less visual foraging and more tactile foraging at night (Hulscher 1974, 1976; Evans 1976; McNeil and Robert 1988; Robert and McNeil 1989, McNeil and Rompé 1995, Rompré and McNeil 1995). Eye morphology and physiology are correlated with nocturnal foraging behavior in many bird species (Rojas De Azuaje et al. 1993; Rojas et al. 1999a, 1999b; McNeil et al. 1999). Shorebirds that used tactile foraging techniques, including Short-billed Dowitchers (*Limnodromus griseus*), American Woodcocks (*Scolopax minor*), and Willets exhibited lower retinal sensitivity and had lower rod:cone ratios compared to those that used visual foraging techniques at night, such as Black-winged Stilts and Wilson's Plovers (*Charadrius wilsonia*; Rojas et al. 1999a, 1999b). Variation in foraging technique between day and night also may be a consequence of variation in prey behavior during the daily cycle, resulting in changes in prey availability. Similar or distinct prey communities may be available to shorebirds in common or discrete habitats between day and night (Thibault and McNeil 1995b, Rompré and McNeil 1995). Overall, shorebird prey were more abundant at night at a Venezuelan lagoon (McNeil et al. 1995), and

two annelid prey species commonly taken by shorebirds in Europe (*Nereis diversicolor*, *Lumbricus terrestris*) also were most available at night (MacLennon 1979, Dugan 1981).

Habitat use.—Although some ponds at JDW were used consistently throughout the daily cycle and the entire breeding season, avocets frequented certain ponds at specific times of the day and some ponds were used predominately during either the early or late portion of the breeding season. Variation in prey community distribution and composition during both the daily and breeding cycle may affect avocet distribution. Habitat use also varied within ponds at JDW as birds were found less often on islands and more often in open water late in the breeding season. Reduced use of islands may be a consequence of nest loss. Avocets commonly nest on islands at JDW, and if early season island nesters lost clutches and failed to renest, we would expect use to shift from islands (incubation) to either shore or open water.

American Avocets, and potentially other waterbirds, do not fit the typical diurnal, nocturnal, or crepuscular paradigm. Rather, avocets practice a labile life history strategy throughout the annual cycle (Evans and Harris 1994, Dodd and Colwell 1996, Hötker 1999, Johnson et al. 2002). Such behavioral plasticity enables birds to profit in the dynamic environments they commonly inhabit. At coastal locations, a labile foraging strategy independent of solar cycle allows avocets to take advantage of tidally induced changes in resource availability (Robert et al. 1989). Further, avocet energy acquisition appears independent of day length, which also may be beneficial to avocets breeding in arid environments. Nocturnal sexual and agonistic behaviors in avocets are sufficiently frequent that further study of avocet reproductive behavior must consider nocturnal habits. The role of nocturnal reproductive behavior should be assessed in species generally perceived as being diurnal.

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PAIR BOND MAINTENANCE IN PILEATED WOODPECKERS AT ROOST SITES DURING AUTUMN

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ABSTRACT.—Individuals in a number of bird species have the opportunity to maintain contact with their mates during nonbreeding periods. This contact may be important to synchronize the partners' reproductive cycles before breeding begins. As a first step toward exploring the function of pair bond maintenance in nonbreeding birds, I studied the behavior of three pairs of Pileated Woodpeckers (*Dryocopus pileatus*) and an unpaired male at roost sites during autumn. At dawn and dusk, paired individuals exchanged visual, vocal, and other acoustical signals identical to those given during the breeding season. Demonstration tapping away from a nest is reported here for the first time. The possible function of these behaviors may be related to monitoring the partner's condition and investing in the pair bond to enhance future reproductive success. *Received 19 September 2002, accepted 01 March 2003.*

The pair bond of many birds is formed each spring as courting birds establish a relationship with their future mate. Once the nesting season ends, many birds cease to maintain the pair bond. However, in a diverse group of species, formation of a pair bond may occur long before spring, and termination of the pair bond at the end of reproduction may not occur (reviews in Oring 1982, Fowler 1995, Black 1996). Future and/or former mates may interact and cooperate with one another on a continuing basis throughout the year, or at least during part of the nonbreeding season. The investment into this relationship by individuals is referred to here as pair bond maintenance.

Advantages of pair bond maintenance outside the breeding season are unclear and poorly documented. Some hypotheses suggest that individuals gain reproductive benefits from spending time with a partner prior to breeding. For instance, pair members familiar with each other may achieve reproductive synchrony earlier or to a greater degree compared to other pairs (Butterfield 1970, Rowley 1983, Ens et al. 1996). Other hypotheses depict the mate as a resource that must be protected, nurtured, and retained in order to avoid high costs that might be involved with the loss of a partner through death or divorce (Ens et al. 1993, Choudhury 1995, Hogstad 1995). These hypotheses are hard to evaluate since in many cases it is not clear which behaviors are involved with pair bond maintenance and how the behaviors might be experimentally manipulated without altering social or environmental conditions. Because different species have various natural histories, the behavioral mechanisms by which pair members of each species can protect, nurture, and gain familiarity with each other differ. Thus an important first step in addressing questions about pair bond maintenance during the nonbreeding season is to document the frequency and context of behaviors that may facilitate pair bond maintenance.

Pileated Woodpeckers (*Dryocopus pileatus*) are thought to pair with the same mate in successive reproductive seasons. Some of these pairs maintain contact with each other during winter while others do not (Bull and Jackson 1995). The nature of this nonbreeding season contact is not well described. However, Pileated Woodpeckers give loud "wuk" vocalizations near their roost sites (Bull and Jackson 1995), and these may help the pair maintain contact with each other (Kilham 1974). "Wuk" calls may be exchanged between pair members in the manner of a duet (Short 1982). Other behaviors, such as head swinging, demonstration tapping, and exchanges of various vocal signals, have been documented as part of courtship (Kilham 1959, 1979).

Because Pileated Woodpeckers usually are found at low densities, and parental investment is substantial and nearly equal between males and females (Short 1982, Bull and Jackson 1995), it seems likely that losing a mate

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through death or divorce would be costly. Thus, monitoring the current mate's condition, even during nonbreeding periods, may be an important investment in future reproductive success. It is in this framework that I discuss behavioral signals observed at roost sites during autumn. I also present data on the characteristics of male and female roost cavities and the timing of roost entry in relation to weather conditions. Both types of data could potentially affect pair interactions.

METHODS

I searched for roost sites of Pileated Woodpeckers in the mixed forests of Acadia National Park, Maine (44° 26′ N, 68° 21′ W), between 12 September and 20 November 1995. Canopy species included red oak (*Quercus rubra*), white birch (*Betula papyrifera*), American beech (*Fagus grandifolia*), and red spruce (*Picea rubens*). Roosting areas (but not the cavities themselves) were relatively easy to find because past wildfires in my study area created a patchy landscape of large-diameter trees where burn intensity was low. Once a roost cavity was found, I observed each individual's behavior during the evening and morning from a position ≥20 m from the tree where each roost hole was located. I used the same observation points each time, and the roosting birds seemed to ignore me. Evening behavioral observations began 90 min before sunset and ended 10 min after roost entry. Morning observations began 30 min before sunrise and ended 10 min after an individual left the roosting area.

I collected data on selected weather variables to determine whether variation in roosting time was related to cloud cover, air temperature, or barometric pressure. Cloud cover was recorded as the percentage of sky obscured at the time of roost entry: clear (0–34%), partly cloudy (35–69%), and cloudy (70–100%). I obtained temperature and barometric pressure readings from a weather station located on the College of the Atlantic campus, 11.6 km from the farthest roosting site. I used ANOVA (SAS Institute, Inc. 1999) to determine whether the timing of roost entry was related to one or more of the weather variables. Because my sample size was too small to employ a repeated measures test, I analyzed each individual's data separately.

During evening observations, I noted acoustical signals, including vocalizations and drumming, and head swinging displays that occurred ≤3 min of roost entry. I chose this time interval because the location of individuals (and thus the identity of those giving signals) was not always known before woodpeckers arrived at the roost tree. During morning observations, I collected behavioral data on individuals for up to 30 min, depending upon how quickly they left the roost area.

RESULTS

I studied eight unmarked individuals, including three male-female pairs (Campus, Point, and Nubble) and two males (Lake and Head) that apparently had no female partners. Five of eight individuals used multiple roost sites, and the number of observations for each individual varied according to how rapidly I could locate the next roost. I identified individuals by sex and location of roosts. Trees with roost cavities usually were clumped, and the data reported here are based on the five patches occupied by the pairs and single males; low coastal mountains separated each patch. I have no evidence that more than two individuals ever frequented the same patch. The maximum distance between known roost cavities within a patch was 350 m, and the minimum distance between the patches I studied was 2.5 km.

The single roosts of one male-female pair (Campus pair) were only 35 m apart and could be monitored concurrently from the same observation point. Other paired individuals roosted 55–135 m from their mate when both roost locations were known.

I found few differences between male and female roost trees. Male and female roosts were in similar species, at similar heights from the ground, and in a mix of live and dead trees (Table 1). However, males appeared to use newer roost cavities than did females. The Campus male's roost was used as a nest during the previous spring, while the Campus female's roost was a nest three springs before (unpubl. data). The two roost cavities used by the Nubble male were excavated within the year, but the Nubble female's roost appeared older. I could not determine the age of the Point woodpeckers' roosts, but the roost cavities of the female had several more entrance

TABLE 1. Characteristics of cavity trees located near Pileated Woodpecker roosting areas during autumn in Maine, 1995.

Location	Cavity occupant	Dates used	Tree species	Tree condition	# entrances	Height of lowest entrance (m)	dbh (cm)
Campus	Male	18 Sept to 20 Nov	Norway maple (*Acer platanoides*)	Live	1	9	42
	Female	25 Sept to 20 Nov	Norway maple	Dead	1	7	45
Point	Male	12 Sept to 30 Oct	Gray birch (*Betula populifolia*)	Dead	2	8	58
	Male	20 Nov	Red maple (*A. rubrum*)	Live	1	16	40
	Female	28 Sept to 5 Oct	Gray birch	Dead	3	7	40
	Female	31 Oct to 4 Nov	Gray birch	Live	5	18	43
	Not used		Gray birch	Dead	1	8	39
	Not used		Gray birch	Dead	1	9	28
	Not used		Red spruce (*Picea rubens*)	Dead	1	15	37
Nubble	Male	21 Oct to 23 Oct	Beech (*Fagus grandifolia*)	Live	1	2	44
	Male	24 Oct to 5 Nov	Beech	Live	1	6	51
	Female	21 Oct to 23 Oct	Red maple	Dead	1	20	53
	Not used		Red maple	Dead	2	15	44
Lake	Male	10 Oct to 19 Nov	Red maple	Dead	2	8	66
	Not used		Red maple	Dead	1	8	40
Head	Male	4 Oct to 9 Oct	Beech	Live	2	5	47
	Not used		Red Oak (*Quercus rubra*)	Live	1	3	42

holes than the male's cavities (Table 1), which could indicate that the ages of her cavities were older than those used by the male. All three pairs excavated new nests within 25 m of a known roost cavity during the spring following my study.

Evening roost entry.—Vocalizations recorded during the 3 min prior to roost entry consisted mostly of "wuk" calls, often combined during a continuous bout of sound lasting 5 s or more. I frequently heard these calls throughout the afternoon as well. The Campus male and female gave "wok" calls, considered a courtship call by Kilham (1959). This pair also gave head swinging displays while on the roost tree, and all paired individuals gave drums or a short distance acoustical signal known as demonstration tapping (Table 2; see Short 1982 for descriptions of these signals). Bouts of tapping took place on the roost tree, sometimes from inside the roost itself. Other instances of tapping involved a series of 2–6 irregularly spaced taps, given on or near the roost tree.

I monitored the roost entry times of the Campus pair on 20 evenings during my eight-week study and found that the female entered her roost 0–47 min before the male (Fig. 1). It is not known what factors contributed to the campus female's decision to roost. Cloud cover, temperature, and barometric pressure together did not explain a significant amount of variation in her roosting time ($F_{4,19} = 0.66$, $P = 0.63$). However, the timing of the Campus male's roost in relation to his mate's roost time was related to cloud cover ($F_{2,19} = 6.88$, $P = 0.007$). This male entered his roost on cloudy days a mean of 11 min ± 4 SE after the female ($n = 7$), but roosted much later on clear days (32 min ± 5 SE after the female, $n = 9$; post-hoc comparison $t = 3.70$, df = 14, $P = 0.002$). The male's activities on clear

days following the female's roosting time took place away from the roosting area, so the reason for his delay was unknown.

In contrast to the uncoordinated movements of the pair on clear evenings, the Campus pair arrived at the roost site together on six of seven cloudy evenings. When the female entered her roost, she looked in the direction of the male as he foraged nearby. Twice the male followed the female to her roost cavity's entrance, and spent several minutes preening there before flying to his own roost for the night. A similar situation was observed between the Nubble pair, except that it was the female who spent time at the opening of the male's roost after he had entered.

Morning roost exit.—All Pileated Woodpeckers occasionally removed sawdust, wood chips, fecal material, or feathers from roost cavities before exiting in the morning at sunrise. Woodpeckers frequently gave "wuk" calls and drums at that time (Table 2). Mates regularly responded to these signals with a similar bout of drumming, vocalization, or demonstration tapping. No published account of Pileated Woodpecker behavior has described demonstration tapping during the nonbreeding period. Below, I describe two of the most extended pair interactions that featured tapping.

On the morning of 4 October 1995, before the Campus female left her cavity, the male flew to near her roost, vocalized, and tapped. The female watched him for 14 min and then spent 6 min removing at least 45 bill-fulls of sawdust from her cavity. She exited her cavity, flew to the male's position, and demonstration tapped three times. The male drummed. She re-entered her cavity and tapped six times from inside. The pair exchanged signals in this manner for another 5 min, then the female flew from the area. The male remained, entered the female's roost cavity, and pecked at the cavity entrance and below the inside sill for 4 min. He then left the cavity and flew in the same direction that the female had gone. He returned, alone, to the female's roost tree 17 min later. He drummed on the outside and re-entered her cavity for 3 min. He gave a string of "wuk" calls on his way out of the cavity, and left the area again.

On the morning of 19 October 1995, the Campus male and female interacted at the male's roost cavity. The male initiated the activity by drumming near his roost tree. The female, who had not yet left her roost cavity, responded with a drum. She then left her roost and flew to the entrance of his roost. The male flew to her position, entered his cavity, and tapped from inside. The female reciprocated with more demonstration tapping. Both birds left the area together.

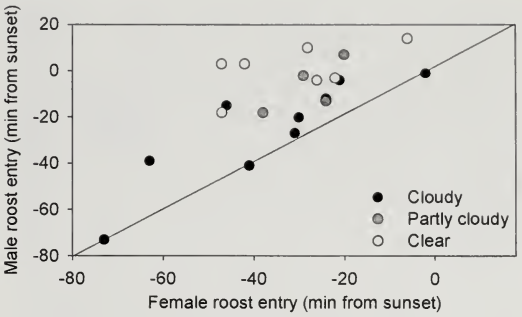

FIG. 1. The female Pileated Woodpecker of the "Campus" pair usually entered her roost before the male entered his, and she preceded the male by the most amount of time on clear evenings. Negative values are minutes before local sunset. Both birds enter their roosts concurrently along the diagonal reference line. Data are from Acadia National Park, Maine, autumn 1995.

The timing of pair member interactions after sunrise depended upon when the individuals left their cavities. The Campus male left his roost a mean of 19 min ± 14 SD (n = 7) before the female. However, the Campus female was awake for a time before she left the roost, as I saw her look out from her cavity a mean of 17 min ± 15 SD (n = 7) before her roost exit. As in the above examples, she spent much of this time in the roost watching her mate and responding to his signals. After both birds had exited their respective roost cavities, the Campus male and female usually left the area together, and limited observations of the other two pairs also suggest that pair members rendezvoused with each other and interacted after leaving their roosts. For example, the Point male always (n = 7) flew in the same direction after leaving his roost, and two vocalizing or drumming Pileated Woodpeckers always were heard within a few minutes of his departure, from the same direction as his departure.

TABLE 2. Signals given by Pileated Woodpeckers at roosts in the evening (roost entry) and morning (roost exit). Values are mean signals/min ± SD and represent the short periods of time when woodpeckers were within 50 m of the roost cavity. Reciprocated signals are those which immediately followed a signal from the mate. Data are from Acadia National Park, Maine, autumn 1995.

	Entry or exit	Campus male $n = 29$ $n = 15$	Campus female $n = 20$ $n = 10$	Point male $n = 12$ $n = 7$	Point female $n = 6$ $n = 7$	Nubble male $n = 5$ $n = 2$	Lake male $n = 7$ $n = 5$
"Wuk" calls	entry	1.47 ± 1.35	0.90 ± 0.33	1.68 ± 1.68	0.84 ± 0.99	0.21 ± 0.45	0.42 ± 0.78
	exit	1.14 ± 0.93	0.27 ± 0.30	1.29 ± 0.48	1.05 ± 1.11	0	0.18 ± 0.42
"Wok" calls	entry	0.15 ± 0.36	0.27 ± 0.45	0	0	0	0
Head-swing bouts	entry	0.18 ± 0.39	0.06 ± 0.24	0	0	0	0
Drumming bouts	entry	0.06 ± 0.36	0.06 ± 0.24	0.09 ± 0.30	0	0.21 ± 0.45	0
	exit	0.60 ± 0.66	0.09 ± 0.30	0.90 ± 1.05	0.27 ± 0.69	1.35 ± 0.63	0
Tapping bouts	entry	0.03 ± 0.18	0.06 ± 0.24	0.18 ± 0.39	0.33 ± 0.51	0	0
	exit	0.18 ± 0.39	0.18 ± 0.39	0	0	0	0
Reciprocated signals	entry	14% of 50	21% of 24	22% of 23	43% of 7	0% of 2	0% of 3
	exit	21% of 32	17% of 6	29% of 17	60% of 10	66% of 3	0% of 1
<10 m association[a]	entry	14%	20%	27%	33%	20%	0%
	exit	20%	30%	14%	14%	0%	0%

[a] Percentage of observations during which mates came within 10 m of one another.

DISCUSSION

I observed Pileated Woodpecker pair members roosting 35–135 m from one another. Other studies confirm that short distances between pair member roosts are common (Hoyt 1957, Short 1982, Bull et al. 1992). It seems likely that pair bond maintenance is facilitated by the proximity of roost sites, since pair members can have greater potential for interaction. Even if roosts are not close, my observations and those of Kilham (1959) suggest that many pairs rendezvous in the morning after roost exit and in the evening before roost entry. Morning and/or evening interactions between mates also have been observed in other species, e.g., Wood Nuthatches (*Sitta europaea*; Radford 1954) and Carolina Chickadees (*Poecile carolinensis*; Pitts 1976).

Mate investment.—Rendezvous and spatial proximity during the day may benefit pair members in a number of ways. Breeding season reproductive benefits might accumulate with long term mate association; shorter term benefits such as mate protection and investment are also likely involved (Kilham 1976). The Campus female always exited in the morning after she saw the male leave his roost, and both Campus and Point females usually roosted earlier in the evening than their partners. Because males of other species protect their mates from predators (McKinney 1985, Hogstad 1995, Hannon and Martin 1996), it is possible that the male woodpeckers were acting as sentries during female roost entry and exit. Predation risk may be relatively high in Pileated Woodpeckers compared to other species (Kilham 1976, Bull et al. 1992). Adult predators include several hawks, owls, martens, and other mammals. Many of these are active at dawn and dusk and are known to lurk near roost cavities (Bull and Jackson 1995). The fact that the Campus pair coordinated roosting times more closely under cloudy conditions might suggest that visibility was lower (Bull 1978), and as a result, predation risk might have been higher on those evenings. In two of my study pairs, males seemed to play the role of sentry, but that does not exclude the possibility of female sentry behavior. For example, one night the Nubble female accompanied the male to his roost before she flew to her own.

Signaling and reciprocation.—Individuals frequently gave vocal and other acoustical signals near roost sites, and these included the "wuk" call and demonstration tapping. Both signals occasionally were repeated back and forth between pair members in the manner of a duet. One explanation for duets and other reciprocated vocal signals between mates during nonbreeding periods is that the signals indicate to nonmates that the territory is occupied by a mated pair and there is little chance that either a mate or the territory may be usurped by an intruder (Hall 2000). However, the tapping signals exchanged by mates were quiet and likely could not be heard by other conspecifics.

A different explanation is more likely. Many investigators regard sexual signals given during the nonbreeding season as part of pair bond formation or maintenance (Butterfield 1970, McKinney 1985, Choudhury and Black 1993). The assemblage of signals I observed during autumn is nearly the same as that exhibited by courting Pileated Woodpeckers during spring, lacking only the crest raising and wing spreading displays (Bull and Jackson 1995). Under the mate familiarity hypothesis, sexual signals given during the nonbreeding season may function to ensure continued familiarity between partners (Ens et al. 1996). This familiarity may improve reproductive success if repeated interaction between partners during the nonbreeding season results in better synchronization of reproductive or hormonal cycles (Hirschenhauser et al. 1999). In the present study, demonstration tapping is a good candidate for having a pair bond function. Woodpeckers regularly exchange taps at nest cavities (Kilham 1979), and it is interesting that the tapping I observed took place only within or immediately adjacent to trees that were past or future nest sites. Tapping thus seems closely tied to reproduction and may play a role in strengthening physiological and social relationships between mates.

At the same time, male-female association during fall (and winter) may aid an individual's effort to assess the quality of its mate. The mate investment hypothesis suggests that the mate is a resource that must be protected, nurtured, and retained in order to prevent its loss (Ekman 1990, Hogstad 1995). If true, pair members may monitor their partner regularly to assess whether the partner's relative quality has changed from the previous day. A partner that does not reciprocate a signal in the expected manner might be in poor health or may not be hormonally synchronized with the signaler. The signaling pair member may respond by changing the nature or intensity of its pair bond maintenance behavior (Hausberger and Black 1990, Hall 2000).

Clearly, more study is needed on Pileated Woodpeckers and other species with long term pair bonds. Brief roost site interactions at dusk and dawn may contribute significantly to pair bond maintenance, even in pairs that do not appear to interact during the rest of the day. Nonbreeding pair bond maintenance of any kind could have significant effects on survivorship and future reproductive success.

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Short Communications

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Vocalizations and Display in the Long-tailed Ground-roller (*Uratelornis chimaera*)

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ABSTRACT.—During three field seasons in southwestern Madagascar we made opportunistic observations and tape recordings of the sounds produced by the Long-tailed Ground-roller (*Uratelornis chimaera*; Brachypteraciidae). Here we present new information on vocal behavior in this species and provide the first documentation of display and nonvocal production of sound by any ground-roller. *Received 17 June 2002, accepted 4 December 2002.*

The ground-rollers (Brachypteraciidae) are socially monogamous, sexually monomorphic, terrestrial, insectivorous birds endemic to Madagascar. Four species inhabit the humid forests of the east, while the Long-tailed Ground-roller (*Uratelornis chimaera*) is endemic to the semi-arid deciduous forests of the southwest (Langrand 2001). All five ground-rollers are highly secretive, such that little is known about their secondary vocalizations and courtship behavior (Langrand 2001). With this in mind, we studied Long-tailed Ground-rollers, collecting data on their vocal repertoire and displays.

During three seasons (September to February, 1997–2000) at Pointe Kilometre 32, north of Toliara in southwestern Madagascar (23° 05′ S, 43° 37′ E; see Seddon et al. 2000 for habitat description) we encountered at least seven different pairs of Long-tailed Ground-rollers. Using a Sennheiser ME67 directional microphone and a WM-D6C Sony Walkman we opportunistically recorded any sounds produced by these birds. From the resulting 70 min of recordings we identified four distinct vocalization types, the temporal and frequency characteristics of which are summarized in Table 1.

One vocalization (the "song") consisted of low-pitched, clipped, and emphatic hooting notes at 1,200–1,400 Hz, with 1–2 harmonics (Fig. 1a), usually delivered in an evenly spaced series (often 8–9 notes, but sometimes as few as 3 or as many as 12; Fig. 2a). Bouts of hooting were given from a concealed perch 2–6 m above the ground, with the vocalizing bird pumping its tail downward slightly in time with each hoot. We recorded bouts at dawn (05:30 to 06:15; GMT +04:00) and at dusk (18:40 to 19:15) lasting up to 20 min. The crepuscular (or nocturnal) timing of these bouts, and the fact that they carry far (audible to human ears for up to 200 m), suggests that they function in mate attraction and/or territory defense (see Catchpole and Slater 1985). Hooting appeared to be performed by only one bird per pair, presumably the male.

A second vocalization given by both sexes consisted of abrupt popping notes, given in couplets, the second note of higher frequency than the first, and often with a single harmonic. This call, previously transcribed as "too-tuc too-tuc too-tuc" (Langrand 2001), is herein referred to as the *tu-tuc* call (Fig. 1b). It was audible over only relatively short distances, and seemed to be given more frequently when pair members were within 10 m of each other.

A third call was a soft muffled *boo* (Fig. 1c), usually given in a series of 2–6, sometimes preceded, followed, or interrupted by *tu-tuc* calls (Fig. 2b). As with *tu-tuc* calls, *boos* were given most frequently on the ground or on low branches ≤2 m high.

A fourth vocalization (Fig. 1d) consisted of a disyllable that was louder, more drawn out, and more emphatic than the *tu-tuc* call, with a higher fundamental frequency for both notes (Table 1), and a more grating tone resulting in a stack of 4–10 harmonics up to about 12 kHz (mean number of harmonics = 5.7 ± 1.2 SD,

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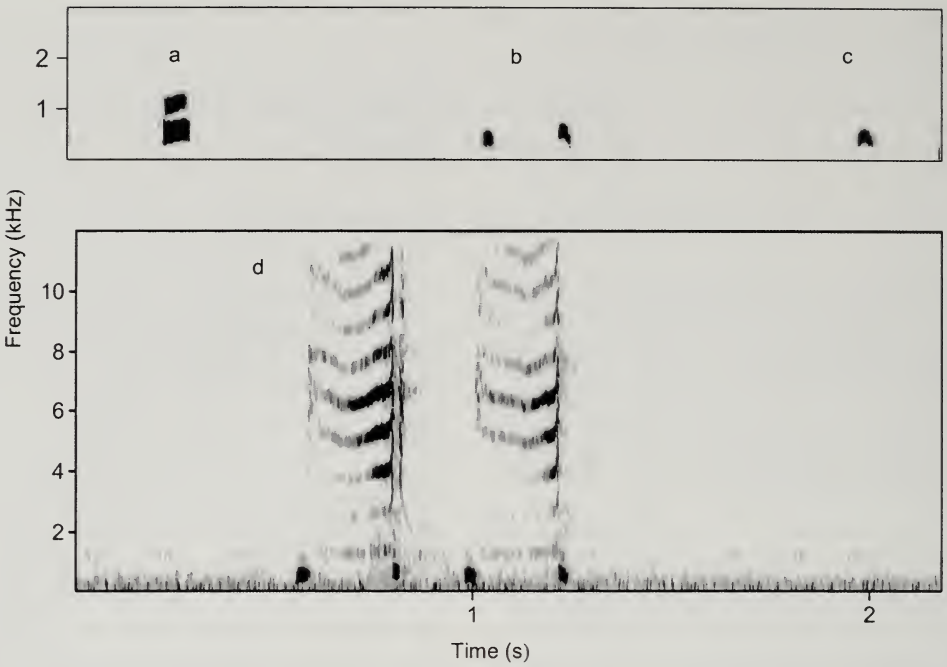

FIG. 1. Composite audio spectrogram of Long-tailed Ground-roller vocalizations: (a) one hoot given by a male (these are always given in series), (b) one *tu-tuc* call, (c) one *boo* call, and (d) one alarm call. All recordings were made by J. A. Tobias in the vicinity of nest holes at Pointe Kilometre 32, north of Toliara, Madagascar, November 2000 to January 2001. Recordings were digitized with a 16-bit acquisition card at a sampling rate of 16,000 Hz. Using the software Avisoft SASLabPro ver. 4.0c, calls were filtered to prevent aliasing and to remove background noise, and spectrograms were generated with the following settings: FFT = 512, bandwidth = 235 Hz, frequency resolution = 31 Hz, frame = 50%, window = FlatTop, overlap = 88%.

n = 17 calls). We refer to this as the "alarm call," as in all cases it was given by adults of both sexes standing alertly or nervously <5 m from a nest burrow.

In January 2001, we observed one Long-tailed Ground-roller in the nest-digging phase of the breeding cycle performing an unusual display involving the repeated nonvocal production of sound. The display was always preceded by a series of *tu-tuc* calls given from the ground, sometimes for several minutes, while the bird halted beneath a low (1–2 m high) branch, tilting its bill so that it pointed almost vertically upward. While standing motionless in this position the bird gradually increased the rate of *tu-tuc* calling to a crescen-

TABLE 1. Temporal and frequency characteristics of Long-tailed Ground-roller vocalizations. Means ± SD are given; different bouts were separated by ≥30 s of silence; syllables are evenly spaced notes wherein internote interval is at least half intersyllable interval. Measurements were taken from spectrograms that were generated from digitized recordings using Avisoft, at the settings listed in Fig. 1. All recordings were made by J. A. Tobias at Pointe Kilometre 32, north of Toliara, Madagascar, November 2000 to January 2001.

	Hoots	*Tu-tucs*	*Boos*	Alarms
Duration of syllable (s)	4.0 ± 1.3	0.27 ± 0.04	0.21 ± 0.07	0.28 ± 0.02
Number of notes per syllable	8.9 ± 2.8	2.0 ± 0.0	2.0 ± 0.5	2.0 ± 0.0
Rate (syllables/min)	3.4 ± 1.0	126 ± 25	8.5 ± 3.4	46.0 ± 2.8
Fundamental frequency (Hz)	305 ± 44	110 ± 2	93 ± 24	253 ± 88
Band width (Hz)	536 ± 82	602 ± 62	504 ± 49	10,600 ± 634
n (syllables, bouts)	18, 10	18, 8	10, 5	17, 2

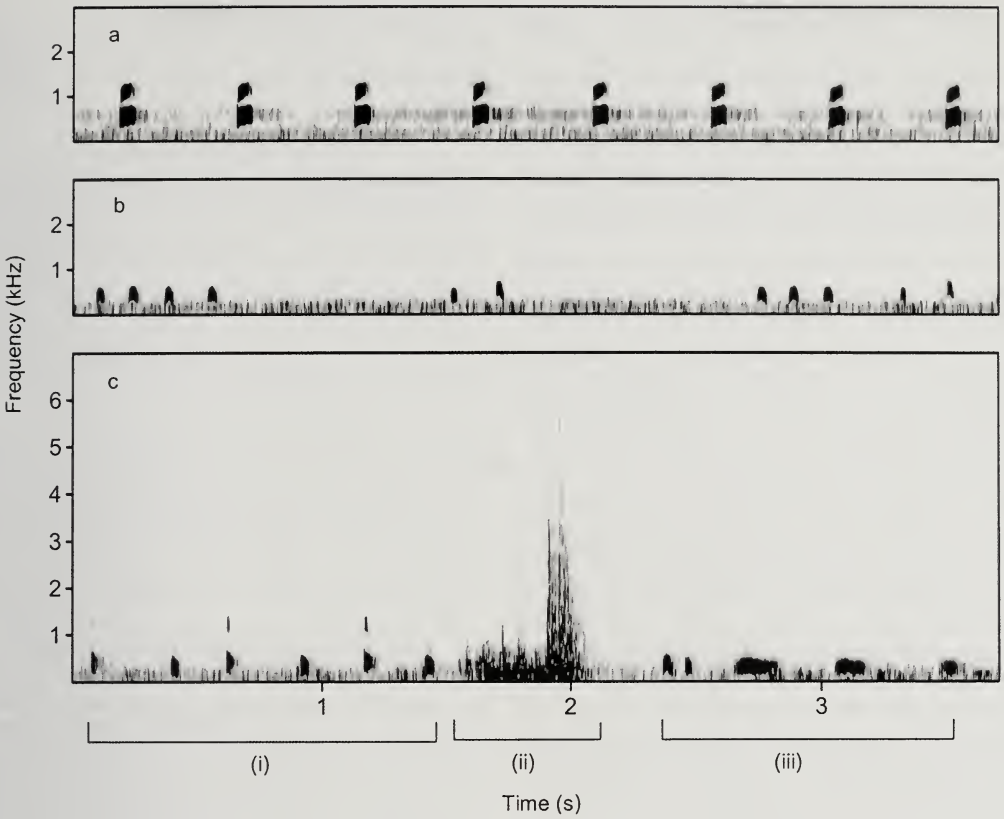

FIG. 2. Audio spectrograms of typical sequences of Long-tailed Ground-roller vocalizations: (a) a song consisting of a series of eight hoots; (b) a sequence of four *boo* calls, a *tu-tuc* call, three more *boos,* and a final *tu-tuc*; and (c) a display sequence consisting of (i) an introductory vocal phrase (a series of three *tu-tuc* calls), (ii) a nonvocal phase (fluttering and then "cracking" wing feathers as bird flies to perch), and (iii) a terminal vocal phrase (a short slightly descending series of *boo* call notes). All recordings were made by J. A. Tobias in the vicinity of nest holes at Pointe Kilometre 32, north of Toliara, Madagascar, November 2000 to January 2001. Spectrograms were produced as in Fig. 1.

do. The terminal phase of this crescendo formed a distinct introductory phase to the display: an accelerating burst of 3–10 *tu-tuc* calls (mean number of calls = 7.1 ± 2.7 SD; mean duration of series = 3.6 s ± 1.8 SD, n = 8 displays) which culminated in a loud ripping and cracking sound as the bird flew steeply up to the branch. This sound obviously was not produced vocally; the ripping always corresponded to the series of rapid wingbeats as the bird ascended to the perch, and the final loud cracking note was simultaneous with the last wingbeat before landing. This sudden and dramatic sound was followed by another vocal phase, a brief series of 3–6 soft *boo* notes lasting for a mean of 1.3 s ± 0.3 SD, the first notes brief and the last more protracted. After perching silently on the branch for 10–120 s, the bird usually dropped back to the ground and repeated the process almost exactly.

Langrand (2001) mentioned a harsh scratching note that sometimes terminated a series of *tu-tuc* calls, but while this undoubtedly refers to the sound described above, he neither mentioned the display nor suggested that the sound was produced nonvocally. Whether the wing tips were struck together to make this sound, or whether it was produced by a whiplash action, was impossible to determine, although the latter case seemed more likely. An audio spectrogram of the display sequence (Fig. 2c) begins with the crescendo in *tu-tuc* calling (i), followed by the nonvocal phase (ii), and finally the short series of *boo*

notes (iii). It also reveals that the nonvocal section (ii) contains six pulses of sound corresponding to the wingbeats; the first five (the ripping sound) are fairly muted and the final one (the "crack") is loud and has a broad bandwidth (mean = 7,542 Hz ± 423 SD).

One male performed this display a total of 20 times during a 50-min period (10:20–11: 10) on 7 January 2001, and three times during 5 min of a prolonged bout of hooting (i.e., singing) four days later. During the first observation period, we broadcast a recording of the display sound through a loudspeaker from a distance of 5 m. The male responded to this by approaching to <2 m from the speaker and increasing his performance rate from 7 displays/20 min to 12 displays/20 min. Throughout both observation periods, the displaying bird was 1–10 m from another individual, which we presumed to be the female due to its smaller size, narrower chest band, and shorter tail (Langrand 2001). On one occasion we saw this probable female perform a very similar display which was quieter in both vocal and nonvocal phases shortly after playback of the display sound. No direct interaction between the two birds was noted.

While the hooting song and alarm call have been reported previously in this species (Langrand 2001), no mention has been made of this highly stereotyped display. Furthermore, this is the first description of a nonvocal sound, or indeed any display produced by this species or any other member of the Brachypteraciidae. "Wing cracking" is a relatively rare phenomenon; it occurs in at least one other coraciiform family, the todies (Todidae; Kepler 2001), as well as a variety of unrelated families such as nightjars (Caprimulgidae; Cleere 1999) and manakins (Pipridae; Prum 1998, Bostwick 2000a). In manakins, nonvocal sounds function in courtship (Bostwick 2000b), and the same is likely in the Long-tailed Ground-roller (although participation by a presumed female is odd). Whether the other reclusive members of the Brachypteraciidae have similar displays remains to be discovered.

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Apparent Cooperative Hunting in Florida Scrub-Jays

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ABSTRACT.—I observed an apparent coordinated attack by a mated pair of Florida Scrub-Jays (*Aphelocoma coerulescens*) on a black racer (*Coluber constrictor*) in southcentral Florida. Depending upon their size, snakes can be either prey or predators of scrub-jays. This medium-sized snake may have been large enough that one bird could not safely subdue it. By coordinating their attack, the birds were able to kill and feed on the snake. This appears to be an example of pair hunting. The cooperative hunting technique, in which two mated birds perform coordinated movements, enables the pair to attack otherwise prohibitively large prey. Both members of the attack benefit by eating the prey. Cooperative hunting has only rarely been described in passerines. *Received 19 November 2002, accepted 11 March 2003.*

Among cooperative breeding birds, coordination of behaviors, such as vigilance and predator avoidance, territorial defense, nest building and maintenance, incubation, and care and feeding of young (see Stacey and Koenig 1990) is widespread; however, cooperative hunting has been observed only in the Harris's Hawk (*Parabuteo unicinctus*; Mader 1976, Bednarz 1988). Cooperative hunting, in which two or more members of a foraging group coordinate their behavior to capture certain prey more effectively (Ellis et al. 1993), is more common among mammals (especially large, social carnivores; Packer and Ruttan 1988) than among birds. It has been described for only a few bird species, mostly raptors (see review in Hector 1986) and has been described in only two passerines: Common Ravens (*Corvus corax*; Maser 1975, Hendricks and Schlang 1998) and Loggerhead Shrikes (*Lanius ludovicianus*; Frye and Gerhardt 2001). Here, I report an instance of apparent cooperative hunting in the Florida Scrub-Jay (*Aphelocoma coerulescens*), a cooperatively breeding passerine.

At approximately 09:55 EST on 1 March 2000, in Lake Placid, Highlands County, Florida (27° 15′ N, 81° 25′ W), I watched a color-banded breeding male Florida Scrub-Jay foraging in a 1-m sand live oak (*Quercus geminata*) shrub. At times he was briefly out of sight, but returned repeatedly to the same point about midway in the shrub. It was early in the nesting season and I presumed he was prospecting for a nest site. Upon examining the potential nest site, I found a small (length 45–55 cm, girth <2 cm) black racer (*Coluber constrictor*) coiled and in an aggressive posture on a dead palmetto (*Serenoa repens*) frond about 0.5 m above the ground in the center of the oak shrub. The jay was repeatedly approaching the snake from below and to one side, always from the inside of the shrub. The snake faced the jay upon each approach, but the jay appeared to direct its bill jabs at the palmetto frond rather than at the snake. During these attacks, I never observed the snake attempt to strike the jay. To reach the snake from opposite sides of the frond, the jay had to move down the shrub and behind the main stem; this usually took 5–7 s, sufficient time for the snake to reorient itself to face the attack from the opposite side of its perch. These alternating, side-to-side attacks continued for approximately 20 min without appearing to escalate in intensity.

At this time, the male jay's color-banded mate flew to the shrub. She approached the snake from above and from the outside of the shrub, the opposite direction from which the male jay had been approaching. The female jay also jabbed at the snake. Her jabs did not make contact with either the snake or the palmetto frond, but she did gain the snake's attention. Consequently, when the male approached, the snake was facing the female and the male directed a bill jab at the body of the snake. The snake appeared to avoid the full impact of the jab and neither jay attempted to move closer to the snake. The snake immediately returned to its coiled, aggressive posture. The female continued to jab at the snake and the male continued to jab at the snake's body whenever the female had the snake's attention. Finally the male jay struck the snake

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forcibly, quickly flinging the snake off the palmetto frond. The snake was momentarily tangled in the oak and the male jay jabbed at it several times before it fell to the ground. The female jay flew from the shrub and the male jay followed the snake to the ground but did not vigorously attack. Only when the female returned to the shrub and appeared to distract the snake again did the male attack the snake. The snake struck the male jay in the breast and the jay jabbed at the snake's head. Within 1–2 s, the jay appeared to have killed the snake. The jay stood over the snake for 10–15 s, looking around, fluffing its feathers briefly, then began pecking at the snake's head. He appeared to eat part of the head, then, using his bill, he dragged the snake out from under the oak shrub. The jay grasped the snake by the body, about 5–6 cm behind the head. Out from under the canopy of the oak shrub, the jay continued to peck at the head of the snake. The jay again grasped the body and flew to the interior of a 3 m scrub oak and perched about 2 m above the ground. The snake was draped over a branch and the jay used its feet to hold the head and, after 15–20 s, the jay began to feed. During this time, the female jay remained perched nearby but never vocalized. After <1 min, the male jay flew to the female and fed her. He returned to the snake and continued to feed. After about 10 min, an extra-territorial jay called nearby and both adults flew, giving their stereotypical territorial display. Neither jay returned to the snake during the next 15–20 min. I returned the next morning and the snake was not visible in the tree. The entire episode, from the time I discovered the male jay already engaged with the snake, until he flew with the snake into the oak tree, lasted nearly 45 min.

The diet of Florida Scrub-Jays comprises mainly arthropods and acorns, but small vertebrates, including snakes, are eaten opportunistically (Woolfenden and Fitzpatrick 1996). Snakes can be either prey or predators of Florida Scrub-Jays, depending upon the size of the snake. Large snakes are mobbed, but the behavior of both the male and female scrub-jays I observed was not consistent with mobbing. Mobbing usually includes bobbing and loud and persistent scolding, but neither jay uttered any vocalizations during this interaction nor did they bob. When mobbing, jays also may jab at perches or even jab at the tail of a snake as it moves away (Woolfenden and Fitzpatrick 1996), but during more than a decade of observations I had never before seen mobbing scrub-jays attack a snake in the manner of these jays. Based on these observations, I concluded that the male jay was attempting to prey upon a relatively large snake, and the female jay decreased the potential risk for the male by distracting the snake.

The behavior of these scrub-jays is consistent with pair hunting, one of several cooperative hunting strategies described for raptorial species, but that could easily apply to carnivorous gleaners (i.e., animals that consume small and nonelusive quarry; Ellis et al. 1993). In this instance, the foraging group consisted of two mated birds that performed coordinated movements that enabled the pair to attack prey successfully that either individual alone might not have been able to subdue, and both members of the attack benefitted by eating the prey. Because cooperative breeders are predisposed to coordinated behaviors, they may be pre-adapted to cooperative strategies, including pair hunting. Some species that exhibit cooperative hunting also demonstrate other coordinated behaviors, as in social carnivores (Packer and Ruttan 1988) and Common Ravens (Maser 1975, Hendricks and Schlang 1998).

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Aerial Foraging Over Open Water by Great Egrets and Snowy Egrets on Schooling Freshwater Fish

Andrew C. Kasner[1,2,3] and Thomas P. Dixon[1]

ABSTRACT.—On 21 June 2002 we observed mixed flocks of Great Egrets (*Ardea alba*) and Snowy Egrets (*Egretta thula*) foraging aerially on shad (*Dorosoma* sp.) forced to the surface by foraging white bass (*Morone chrysops*) at the Richland-Chambers Reservoir in Freestone County, Texas. These events occurred over open water ranging from 3–12 m deep during a 2-h period of observation. Egrets foraged exclusively by hovering about 3–5 m above the water and then dipping to capture shad. Foraging behavior was interspersed with intervals of vigilance on a nearby shoreline. Here we provide a detailed record of the temporarily exclusive use by egrets of this rare foraging method in fresh water, in water of such depth, and on live schooling prey over open water. *Received 9 July 2002, accepted 22 February 2003.*

Egrets exhibit a variety of foraging behaviors (Parsons and Master 2000, McCrimmon et al. 2001), with detailed descriptions given by Kushlan (1976) and Willard (1977). Many of the behaviors in their repertoire are used only rarely. The most common behaviors reported for Great Egrets (*Ardea alba*) are Stand and Wait and Wade Slowly (Kushlan 1976, Willard 1977, Rodgers 1983), while Stand and Wait, Wade Slowly, Active Pursuit, and Foot-Stirring are most commonly used by Snowy Egrets (*Egretta thula*; Kushlan 1976, Willard 1977, Rodgers 1983). Kushlan (1976) described several types of aerial foraging. Great and Snowy egrets may grab prey while in direct flight by skimming the water surface briefly, or they may give chase in the air when pursuing prey during wade foraging. Rarely, they hover over shallow water and plunge toward the surface of the water to grasp prey with their bills (Dipping; Kushlan 1976, N. A. Edelson and M. W. Collopy unpubl. data). Aerial foraging is used infrequently under special circumstances (Rodgers 1983). Aerial foraging by Great and Snowy egrets represented only 1–5% of all foraging behaviors during 1,380 h of observation over 4 years (Willard 1977). Rodgers (1983) observed aerial foraging by both species <1% of the time during a 4-year study, while Kent (1986) did not report the behavior in Snowy Egrets during a 1-year study. Individual egrets generally flew a short distance after wading (chasing escaped prey) and captured prey while hovering over shallow water (Willard 1977, Rodgers 1983, Kent 1986). Rodgers (1974) reported a mixed flock of gulls, terns, Great Egrets, and Snowy Egrets following shrimp trawlers and hovering over the surface to gather dead fish (not live schooling fish as in this study) discarded by shrimpers in shallow water (1–2 m). Egrets were responding to the presence of trawlers and other waterbirds visible at a distance from adjacent colonies (Rodgers 1974). N. A. Edelson and M. W. Collopy (unpubl. data) observed that Great and Snowy egrets foraged

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aerially in fresh water after perching in flooded trees in Florida; however, the behavioral description lacked detail and seemed most similar to Dipping, as described by Kushlan (1976). Takita et al. (1984) reported aerial foraging by Snowy Egrets on fish spawning schools in a shallow coastal marsh, but other foraging tactics were used as well. In all of the studies cited above, with the exception of Rodgers (1974) and N. A. Edelson and M. W. Collopy (unpubl. data), aerial foraging was not used exclusively and all aerial foraging was observed in marine habitats. The objective of this paper is to report Great and Snowy egrets using an aerial foraging method that is rarely observed (and presumably rarely utilized) in the field.

On 21 June 2002 from 18:00 to 20:00 CST, we observed a mixed flock of Great Egrets and Snowy Egrets foraging aerially on shad (*Dorosoma* sp.) forced to the surface by foraging white bass (*Morone chrysops*) at Richland-Chambers Reservoir in Freestone County, Texas (31° 57′ N, 96° 06′ W). Egrets hovered about 3–5 m above the water surface and dove feet first toward the surface, flaring the wings to brake and tilting the body forward. They struck at the water using their bills to capture schooling shad that had been forced to the surface. Foraging events occurred over open water ranging from 3–12 m deep. This was the only foraging behavior used by the egrets between bouts of vigilance on the nearby shoreline, approximately 50–100 m away, depending upon the location of the surfacing fish school. Six Great Egrets and five Snowy Egrets stood vigilant on the shoreline when schooling fish were not surfacing. Although sufficient shallow water habitat was present for wading and foraging, we observed no egrets foraging while they stood on the shoreline during the 2-h period. With the appearance of surface activity indicative of a school of foraging fish, some or all of the egrets left the shoreline and flew to the schooling fish, forming a flock of 6–11 birds. Although fishermen were present in boats, the egrets appeared to respond only to the surface disturbance created by schooling fish. Egrets always reached surfacing fish several minutes before fishermen arrived. This behavior was repeated several times during the 2-h period.

Although a few records of similar egret foraging behavior exist (Rodgers 1974, Takita et al. 1984, N. A. Edelson and M. W. Collopy unpubl. data), our observations represent a record of the temporarily exclusive use by egrets of this rare foraging method in fresh water, water this deep, and on live schooling fish forced to the surface by piscine predators. All previous reports of aerial foraging were in shallow coastal habitats (Rodgers 1974, 1983; Willard 1977; Takita et al. 1984), except that N. A. Edelson and M. W. Collopy (unpubl. data) observed the behavior in fresh water. Further observation in the field is necessary to assess the frequency of aerial foraging by egrets, and detailed studies would be useful in determining the energetic value of aerial foraging to egrets as they employ this technique to take advantage of ephemeral prey resources.

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Relationship of Vertebrate Prey Size to Transport Mode and Distance in the Northern Shrike

Remo Probst,[1,3,4] Stefan Wegleitner,[1] and Rudolf Schmid[2]

ABSTRACT.—This report presents experimental data on the transport of vertebrate prey by the Northern (Great Grey) Shrike (*Lanius excubitor*). The species is known to use three modes of transport: carrying prey exclusively with the bill, exclusively with the feet, and by transferring the prey from bill to feet while in flight. Shrikes often transport their prey a short distance from the point of capture (initial distance), followed by the longer flight to the impaling site (long distance). We found that the overall distance (initial plus long) and long distances, but not the initial distance, decreased with increasing prey weight. Greater weight of the prey coincided with reduced use of bill-only transport. The results reveal that Northern Shrikes are well adapted to carry their most common vertebrate prey, voles of the genus *Microtus*. *Received 16 September 2002, accepted 01 March 2003.*

The Northern (Great Grey) Shrike (*Lanius excubitor*) is a Holarctically distributed raptor-like passerine (Cade 1995) that inhabits a variety of semi-open landscapes (Lefranc and Worfolk 1997, Harris and Franklin 2000). Individuals defend large territories, sometimes exceeding 100 ha during winter (Schön 1994a). Although capable of a variety of hunting techniques, the species is primarily a "sit and wait" predator (Glutz von Blotzheim and Bauer 1993). Prey include arthropods, passerine birds, and various small mammals of which *Microtus* species represent most of the total biomass (66–99%; Lefranc and Worfolk 1997).

Because shrikes need to impale vertebrate prey in order to dismember them (Cade 1967, Schön 1996), there is a year round necessity for carrying prey to an impaling site, usually a thorny hedge-like structure (Panow 1996). Three modes of transport are known for the Northern Shrike: carrying prey exclusively with the bill, exclusively with the feet, and transferring prey from the bill to feet while in flight (Glutz von Blotzheim and Bauer 1993).

There are numerous reports in the literature of Northern Shrikes handling their prey (Cade 1967, Grönlund et al. 1970, Ullrich 1971, Olsson 1985, Sonerud 1989), but to date there has been no quantitative study of prey transport in this species. However, this subject has been investigated in the Loggerhead Shrike (*Lanius ludovicianus*; Yosef 1993), a bird slightly smaller than the Northern Shrike and less dependent upon small vertebrates (Lefranc and Worfolk 1997). However, voles, reptiles, and songbirds regularly are taken as prey. Yosef (1993) observed that Loggerhead Shrikes often carry their prey a short distance from the point of capture (initial distance), and subsequently transport the prey a longer distance to the impaling site (long distance).

In Northern Shrikes, prey transport can be either a one-step (an uninterrupted overall distance) or a two-step (initial and long distance) process. To examine the relation of vertebrate prey size to transport mode and distance in the Northern Shrike, we undertook an experiment in which we offered laboratory mice (*Mus musculus*) to free-ranging individual shrikes.

METHODS

We performed the experiment during December 2000 and January 2001 in eastern Austria. The boundaries of the study area (centered on 48° 27′ N, 16° 52′ W) were presented by Kaplan (1999). Terrestrial habitats within the study area ranged from riverine forests to various types of open landscapes (Zuna-Kratky 1999). During the breeding season, Northern Shrikes typically inhabit wet, mowed meadows and agricultural stretches rich in fallow land (Probst 1999), while during winter they inhabit extensive stretches of cultivated land with a high proportion of meadows (Zuna-Kratky et al. 2000).

We mapped the territories of shrikes win-

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TABLE 1. Distances flown and transport modes used by Northern Shrikes in eastern Austria, December 2000 to January 2001, linearly regressed on mouse weights. Overall distance was the distance from prey capture to the impaling site. The overall distance could be covered in a single flight, or by a short initial flight followed by a longer flight to the impaling site. Transport modes included carrying prey in the bill only ("bill"), in the feet only ("feet"), and by transferring prey from bill to feet ("switch"). Probabilities for multiple comparisons of transport modes were Bonferroni adjusted.

		y-intercept		Slope				
Criterion	*n*	Coefficient	SE	Coefficient	SE	r^2	*F*	*P*
Overall distance	68	333.1	43.2	−4.439	1.234	0.16	12.94	0.001
Initial distance	31	47.7	19.0	−0.121	0.598	0.00	0.05	0.840
Occurrence[a]	68	0.7	0.1	−0.008	0.004	0.05	3.62	0.060
Bill versus switch[b]	30	1.4	0.1	−0.025	0.005	0.53	31.37	0.000
Long distance	68	296.5	42.6	−3.986	1.217	0.14	10.73	0.002
Bill versus feet[c]	19	−0.3	0.1	0.026	0.003	0.76	56.72	0.000
Bill versus switch[d]	59	0.3	0.1	0.016	0.003	0.30	24.65	0.000
Feet versus switch[e]	55	1.1	0.1	−0.007	0.003	0.08	4.41	0.040

[a] Dummy-coded with absence of initial distance = 0 and presence = 1.
[b] Transport modes during initial distance flights dummy-coded with bill = 1 and switch = 0.
[c] Transport modes during long distance flights dummy-coded with bill = 0 and feet = 1.
[d] Transport modes during long distance flights dummy-coded with bill = 0 and switch = 1.
[e] Transport modes during long distance flights dummy-coded with feet = 0 and switch = 1.

tering in the study area (RP unpubl. data) and although we did not band individuals, it was possible to distinguish them by the shape of the eye masks and by the wing patterns (Schön 1994b). We offered 68 mice to a total of 22 shrikes. Mice were weighed with an electronic digital balance (±1 g); their sizes ranged from 8.0–64.0 g. We measured distances over which shrikes carried the mice with an optical range finder (±1 m).

We calculated simple linear regressions to evaluate the data. In each case, the requirements of independence and constant variance were met. We evaluated the outcome of the pairwise comparisons with Bonferroni correction. Presence-absence data and different transport modes were represented by dummy-coding (Fisher and van Belle 1993; for assignments see Table 1). Calculations were performed with SPSS ver. 9.0.1. statistical software (SPSS, Inc. 1999).

RESULTS

The results of the regression analyses are presented in Table 1. Long distance (mean 169.2 m ± 18.7 SE, range 2–762 m) and overall distance (maximum 815 m) were significantly negatively correlated with mouse weight, but initial distance (mean 51.1 m ± 8.0 SE, range 2.5–179 m) was not. With low mouse weights there was a greater tendency for transport to be two-stepped. Heavier loads were significantly associated with the occurrence of bill-to-feet transport. The initial distance during bill-only transport was 42.3 m ± 8.8 SE (range 2.5–118 m, $n = 19$), and during bill-to-feet transport was 58.1 m ± 14.4 SE (range 15–179 m, $n = 11$). The mean prey weight during bill-only transport was 20.8 g ± 1.9 SE (range 10–40 g) and during bill-to-feet transport was 41.6 g ± 3.6 SE (range 16–54 g). Feet-only transport was excluded from this analysis because of insufficient sample size ($n = 1$).

There was evidence to suggest that shrikes with heavy loads took off from the ground carrying mice in their feet, but this tendency was not significant at the level we selected ($P = 0.040$ for transport mode I; Table 1). However, as prey weight increased, long distances were covered significantly more often by either bill-to-feet or feet-only transport ($P < 0.001$ for transport modes II and III; see Table 1). The mean long distance flown was 155.2 m ± 37.5 SE (range 45–446 m, $n = 12$) during bill-only transport, 173.3 m ± 22.9 SE (range 2–762 m, $n = 48$) during bill-to-feet transport, and 165.1 m ± 62.5 SE (range 49–582 m, $n = 8$) during feet-only transport. The prey weighed 15.2 g ± 1.4 SE (range 8–26 g) during bill-only transport, 34.1 g ± 1.9 SE

(range 14–64 g) during bill-to-feet transport, and 44.2 g ± 4.3 SE (range 24–63 g) during feet-only transport.

DISCUSSION

Transport modes clearly are related to prey weight; increasing weight led to reduced use of bill-only transport. Our failure to find a significant difference between the feet-only and bill-to-feet transport during long distance flights may be an artifact of the experimental design. As mice weighing more than 64.0 g were not available, we could not provide prey items heavier than a central European Northern Shrike (mean body mass = 65 g; Schön 1996). Therefore, it is possible that a threshold weight was not reached. A similar experiment with Loggerhead Shrikes (mean body mass = 48 g) revealed that prey about 1.3 times the species' body mass were carried (Yosef 1993). If the same were true for the larger Northern Shrike, it would be able to transport prey up to about 85 g. Northern Shrikes have been observed to transport prey as large as an adult Song Thrush (*Turdus philomelos*; about 70 g; Niendorf 1970), although one individual was not able to lift a young rat (*Rattus rattus*) weighing 95 g (Krauβ 1981). The species most often preyed upon by European shrikes, common voles (*Microtus arvalis*) and field voles (*Microtus agrestris*), have adult weights of about 18–51 g and 23–57 g, respectively (Niethammer and Krapp 1982). Our results suggest that despite the rather large territories it inhabits, the central place foraging Northern Shrike (Sonerud 1989) is well adapted to carry prey the size of *Microtus* voles.

Bill-only transport may be advantageous to shrikes when they begin and end a flight. However, further investigations of other possible factors (e.g., aerodynamic aspects), are warranted. Moreover, constraints other than biomechanical ones may influence the trade off among transport modes. For example, bill-only transport may obstruct the shrike's vision. This is important as shrikes must avoid predation as well as kleptoparasitism (Olsson 1985, Yosef and Pinshow 1989).

Overall and long distances, but not initial distance, decreased with increasing prey weight. Transportation of heavy loads incur higher energetic costs, so distances flown with heavy loads should be minimized. During winter, when Northern Shrikes use a relatively large number of feeding places (4–5 main sites; Schön 1994a) they often reduce travel costs by choosing nearby impaling sites. Flying an initial distance might be more influenced by factors other than prey weight (Korpimäki et al. 1994). For example, shrikes frequently carried prey to a nearby perch offering a commanding view of the surroundings, such as a wire, which may be interpreted as antipredator behavior. Initial distances are flown less commonly with large prey items (i.e., large prey commonly are transported in a single step), probably to reduce energetically costly activities of handling and traveling.

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Predation on Birds by a Cuckoo (Cuculidae), Mockingbird (Mimidae), and Saltator (Cardinalidae)

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ABSTRACT.—We report three unusual cases of predation in which birds of insectivorous or omnivorous species preyed upon smaller birds in El Salvador, Central America. A Squirrel Cuckoo (*Piaya cayana*) fed on a netted Indigo Bunting (*Passerina cyanea*); a Blue-and-white Mockingbird (*Melanotis hypoleucus*) chased, killed, and carried off a probable juvenile Rufous-collared Sparrow (*Zonotrichia capensis*); and a Black-headed Saltator (*Saltator atriceps*) fed on a netted Cinnamon Hummingbird (*Amazilia rutila*). Preying upon birds has not been reported previously in any of these species. Evidence suggests that the Squirrel Cuckoo and the Blue-and-white Mockingbird may prey on small birds or other vertebrates with some regularity, while the saltator may have consumed the hummingbird due to non-natural conditions. *Received 21 October 2002, accepted 10 March 2003.*

The feeding habits of many Neotropical bird species are poorly understood. During ornithological studies of birds in El Salvador during the past 30 years, we have encountered three odd instances of birds consuming smaller avian prey. One of the three predators involved, the Squirrel Cuckoo (*Piaya cayana*, Cuculidae), is principally insectivorous (Stiles and Skutch 1989). The other two predators, the Blue-and-white Mockingbird (*Melanotis hypoleucus*, Mimidae) and the Black-headed Saltator (*Saltator atriceps*, Cardinalidae), are presumed omnivores; although little is known about these two species, most members of their families are frugivorous and insectivorous (Bent 1948, 1968). We present each case below.

Squirrel Cuckoo preys on bunting.—On 28 February 1974, at Hacienda Los Pinos near Tierra Blanca, Usulután, El Salvador (13° 20′ N, 88° 40′ W; elevation 50 m), WAT flushed a Squirrel Cuckoo from a netted Indigo Bunting (*Passerina cyanea*) on which it was feeding and which it may have killed in the net. At the time of discovery the cuckoo had eaten much of the bunting's head. Feeding on netted birds has been reported for other cuculids: Greater Roadrunner (*Geococcyx californianus*; Barclay 1977) and Smooth-billed Ani (*Crotophaga ani*; Gill and Stokes 1971).

A Squirrel Cuckoo is about nine times larger than an Indigo Bunting. In El Salvador, a Squirrel Cuckoo collected by OK weighed 122.5 g. Indigo Buntings wintering there weighed a mean of 13.6 g ± 0.9 SD (n = 14; OK unpubl. data).

Other observations suggest that Squirrel Cuckoos regularly may take vertebrate prey. On 2 May 1979, WAT saw a Squirrel Cuckoo at Hacienda Los Pinos carrying a slender, pale green reptile, either a young iguana (*Iguana iguana*) or a snake, which hung down about 10 cm from one side of its bill; the cuckoo paused briefly while it hammered its prey before flying away. Small lizards have been taken by Squirrel Cuckoos across a wide geographic area (Wetmore 1968, Meyer de Schauensee and Phelps 1978, Stiles and Skutch 1989, De Vasconcelos 1998). On 21 March 1979, WAT saw a Squirrel Cuckoo land beside an injured Melodious Blackbird (*Dives dives*), but the cuckoo was frightened away before any interaction took place. Birds and birds' eggs have been reported in the diet of several cuculids (Bent 1940; Sick 1993; Hughes 1996, 1997, 1999, 2001; Eitnear and Tapia 2000), but not previously in the genus *Piaya*.

Blue-and-white Mockingbird preys on sparrow.—On 29 May 1971, at Cerro Verde tourist park, Santa Ana Dept., El Salvador (13° 50′ N, 89° 38′ W; elevation 2,000 m), a jay-sized bird flew past WAT in pursuit of a sparrow-sized bird. The pursuer initially was about 2 m behind and rapidly closing. Both birds sud-

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denly dropped to a terrace of clipped grass 30 m in front of WAT. The smaller bird seemed to drop of its own volition but may have been knocked down. Moments later two more sparrow-sized birds landed nearby, noticed the observer, and flew away silently. WAT then noticed that the larger bird was a Blue-and-white Mockingbird, standing erect and alert. The smaller bird, apparently lifeless, lay on its side. It appeared to be a juvenile Rufous-collared Sparrow (*Zonotrichia capensis*), a common species in the park. The mockingbird picked up its victim, the body hanging limply from each side of its bill, and flew to a nearby low tree. As it flew, the mockingbird uttered the melodious phrases typical of the species. After a brief pause, it flew farther into the woodland, repeating the same phrases. It was not determined if or how the sparrow was consumed.

Blue-and-white Mockingbirds are more than four times larger than juvenile Rufous-collared Sparrows. At Cerro Verde, El Salvador, Blue-and-white Mockingbirds had mean weights of 68 g ± 5.1 SD (n = 20, WAT unpubl. data). The mean weight of juvenile-plumaged Rufous-collared Sparrows at that location was 17 g ± 2.1 SD (n = 4). In comparison, adult sparrows weighed 20 g ± 1.4 SD (n = 85).

We found no published record of comparable predatory behavior in the genus *Melanotis*. Skutch (1950) described the mockingbird's food as small fruits and small invertebrates obtained from leaf litter. At Cerro Verde the species feeds extensively on small fruits (WAT unpubl. data). We also found no reference to similar predatory behavior (with birds as prey) on the part of other mimids, although Northern Mockingbirds (*Mimus polyglottos*) will catch insects on the wing (Derrickson and Breitwisch 1992). K. C. Derrickson (pers. comm.) once observed a Northern Mockingbird chase a Brown-headed Cowbird (*Molothrus ater*), pin it to the ground, and repeatedly peck at it. The cowbird was not killed, however, in that instance. In the Galapagos Islands, endemic mockingbirds (*Nesomimus* spp.) have learned to feed on seabird eggs (Bowman and Carter 1971). Mimids occasionally have preyed upon vertebrates, other than their eggs; Bent (1948) listed tree frogs, small lizards, and small snakes among the foods of Northern Mockingbirds and Brown Thrashers (*Toxostoma rufum*), and mentioned that Gray Catbirds (*Dumetella carolinensis*) were known to catch fish in shallow water.

The Blue-and-white Mockingbird displayed impressive dexterity. We could not easily dismiss this instance of predation as atypical. The swift pursuit, the sudden check, and the quick drop to follow the prey resembled the behavior of an accipiter or a shrike. The actual kill must have been swift, perhaps the snapping of the cervical vertebrae, in shrike fashion. Moreover, there was no hesitation or fumbling when lifting the victim; the mockingbird slid its mandible smoothly beneath the limp body and raised it with the weight seemingly well balanced. The prey was a juvenile sparrow, probably fledged at most a few days earlier, and thus may have been an easy target.

We report here some evidence, albeit weak, that Blue-and-white Mockingbirds may prey regularly on birds during the breeding season. Several times WAT observed incubating Green Violet-ears (*Colibri thalassinus*) react sharply, craning and peering about nervously, whenever a Blue-and-white Mockingbird vocalized nearby; this same reaction occurred upon the approach of Bushy-crested Jays (*Cyanocorax melanocyaneus*), which probably are nest predators. On one occasion a foraging Blue-and-white Mockingbird elicited distress calls from a pair of Orange-billed Nightingale-Thrushes (*Catharus aurantiirostris*) and scolding notes from a pair of Plain Wrens (*Thryothorus modestus*) that had nests in the thicket visited by the mockingbird.

Black-headed Saltator preys on hummingbird.—On 4 July 2001, at Finca Santa Isabel, Cantón El Volcán, San Miguel Dept., El Salvador (13° 28′ N, 88° 17′ W; elevation 750 m), OK netted a Cinnamon Hummingbird (*Amazilia rutila*) in a shaded coffee plantation. The hummingbird was found dead in the net, with a crushed skull. The net also caught a Black-headed Saltator, immediately next to the hummingbird. Dissection showed that the saltator ingested part of the hummingbird's head, including an eye and feathers. The saltator and the hummingbird were preserved (Univ. Kansas Natural History Museum catalog numbers 93751 and 94120, respectively). The saltator weighed 80.0 g, and was an adult male with enlarged testes. The hummingbird,

a male, was not weighed, but conspecifics collected in El Salvador had a mean weight of 4.5 g ± 0.3 SD (n = 7, OK unpubl. data). Although the evidence suggested the net entangled the saltator while it attempted to prey upon the hummingbird, it also was possible that the saltator entered the net by chance, within striking distance of the hummingbird.

We are aware of no other cases of cardinalids feeding on other birds, and only one instance of feeding on a vertebrate: a Northern Cardinal (*Cardinalis cardinalis*) was observed eating a mouse (Bent 1968). Most cardinalids, including saltators, feed on hard seeds, fruits, insects, and occasionally flowers and leaves (Skutch 1954, Bent 1968, Stiles and Skutch 1989, Munson and Robinson 1993, Bosque et al. 1999). Skutch (1960) reported a Buff-throated Saltator (*Saltator maximus*) near the nest of a Royal Flycatcher (*Onycorhynchus coronatus*) eliciting a fierce attack from the male flycatcher, suggesting that saltators may be recognized as nest predators.

In summary, we observed a Squirrel Cuckoo, a Blue-and-white Mockingbird, and a Black-headed Saltator engage in opportunistic predation of smaller birds, two of which were caught in mist nets, and one of which appeared to be a recently fledged juvenile. These behaviors suggest that those species may be broader omnivores than previously believed. While traditional predators of birds, such as raptors and carnivorous mammals, may attack netted birds with regularity, we believe attacks by cuculids and cardinalids on netted birds to be rare, although we cited two previous reports of attacks by cuculids.

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Magellanic Woodpecker Frugivory and Predation on a Lizard

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ABSTRACT.—I report observations of fruit consumption by Magellanic Woodpeckers (*Campephilus magellanicus*) and an opportunistic predation on a lizard (*Liolaemus* sp.) by an adult male. During normal feeding activities, the woodpecker snatched from a bark crevice of a lenga (*Nothofagus pumilio*) tree a lizard, which he then beat until stunned or dead, before flying off carrying the reptile. Frugivory, although undocumented for this species, is widespread among picids. Conversely, this apparently first observation of a Magellanic Woodpecker preying on another vertebrate adds to a few known cases of vertebrate predation by woodpeckers. *Received 6 August 2002, accepted 22 February 2003.*

Weighing 276–363 g, the Magellanic Woodpecker (*Campephilus magellanicus*) is the largest Neotropical picid (Short 1982). It is restricted to the Austral Temperate Forests of Chile and Argentina (35–56° S), where it is found mostly in forests dominated by southern beeches (*Nothofagus* spp., Fagaceae; Short 1970, Vuilleumier 1985). While it has been of interest to ornithologists for several decades, little research has been conducted on this species, and knowledge of its natural history is only rudimentary. Since 1998, I have been studying the breeding biology and nest site selection of this woodpecker in forests in northwestern Argentine Patagonia. While conducting this study, I made opportunistic observations of unusual feeding habits of this species, which, along with related data from other sources, are reported here.

This species obtains its food at sites as diverse as tree trunks, small to large branches, fallen logs, and even the ground (del Hoyo et al. 2002), thus occupying a broad "woodpecker niche" (Short 1970). Although studies of its diet are lacking, it had been assumed to be composed exclusively of invertebrates (Grigera et al. 1994, Rozzi et al. 1996), mainly grubs and adult beetles (del Hoyo et al. 2002). Other arthropods consumed include arachnids, dipterans, and ants (pers. obs.).

Despite documentation only of arthropods as food of the Magellanic Woodpecker, there is increasing evidence of occasional frugivory in this species from different geographical locations. Since 1998, I witnessed adults and juveniles of both sexes opportunistically pecking the juicy berries of saloll bushes (*Berberis serratodentata*) from the ground layer of lenga (*Nothofagus pumilio*) forests at three different locations (38–42° S) in Argentina. On April 1985, A. Ruffini (pers. com.) observed five Magellanic Woodpeckers eating the fruits of maitén trees (*Maytenus boaria*, Celastraceae) in a maitén-ñire (*Nothofagus antarctica*) forest at Isla Victoria (41° 00′ S, 71° 30′ W), Nahuel Huapi National Park, Argentina. The woodpeckers were observed for 45 min, during which time they alternated between eating fruit in maitén trees and gleaning insects in ñires. During March 1999, L. Sympson (pers. com.) observed four woodpeckers consuming fruits of maitén trees in an

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ecotonal forest where mature maitenes were dominant, in Los Alerces National Park (43° 00′ S, 71° 70′ W), Argentina. The woodpeckers fed on fruits for nearly 30 min, flying from one maitén to another and pecking the fruits, sometimes by hanging from twigs. Meanwhile, they apparently sought no invertebrate prey in woody substrates. P. McBride (unpubl. data) observed during late austral summer, 1996, Magellanic Woodpeckers eating the berries of calafate bushes (*Berberis buxifolia*, Berberidaceae) by pecking them from the forest floor litter in central Tierra del Fuego (approximately 54° 00′ S, 68° 00′ W), Argentina. Willson et al. (1994, M. Willson pers. com) consider this woodpecker an occasional seed disperser in Isla Grande de Chiloé (41° 55′ S, 73° 35′ W), Chile.

Although not previously documented for this woodpecker, frugivory is widespread among picids, and even the very specialized wood pecking species (i.e., *Campephilus* and *Dryocopus* spp.) are opportunistic to some extent and may forage at times for fruits (Short 1982). Even though most woodpeckers do feed on insects much of the time, most of them have a diverse diet, and practically all members of the Picidae for which adequate information is available ingest some plant material, just as other piciforms feed diversely at times on animal as well as plant items (del Hoyo et al. 2002). Conversely, reports of consumption of food items other than arthropods or vegetable matter are not common for picids. So far as known, these include a relatively small number of picid species that occasionally capture a lizard or frog (or mice, by the extremely omnivorous Red-headed Woodpecker, *Melanerpes erythrocephalus*), and many picids that regularly prey on the nestlings and eggs of other birds (del Hoyo et al. 2002). Also, some members of the Picidae opportunistically visit artificial bird feeders and remove pieces of raw meat hung out to dry (del Hoyo et al. 2002). Recently, the Pileated Woodpecker (*Dryocopus pileatus*) has been reported scavenging on carcasses (Servín et al. 2001).

On 27 December 2001, while following a solitary male Magellanic Woodpecker, I witnessed the bird capture an adult lizard (*Liolaemus* sp.). The observation occurred at 6:50, at approximately 1,450 m elevation, in pure old growth lenga forest, 15 km southeast of Bariloche city (41° 15′ S, 71° 16′ W), Argentine Patagonia. This forest averages 20 m tall and has an open understory.

After 20 min of normal feeding activities, which usually include pecking and probing the tree surface and scaling off bark, lichens, and mosses, the bird found and seized with his bill a lizard inside a bark crevice located 7 m from the ground on a lenga tree. Although almost twice the length of the bird's bill, the lizard provided little resistance, as it was nearly immobile from the cold ambient temperature (2° C). When the Magellanic Woodpecker secured the lizard with his bill, he began to make a series of lateral head pecking movements, similar to those used to deliver blows from each side alternately when chiseling out a piece of wood (typical of this and other specialized wood pecking Campephilini picids; Short 1982). As the woodpecker climbed down the tree, he repeatedly beat the lizard against the trunk. Once on the ground, the woodpecker dropped the apparently lifeless lizard (which had lost its tail), looked at it for a few seconds, and then picked it up and flew off with it in an unsteady flight. The whole sequence lasted about 50 s.

These are the first accounts of frugivory for the Magellanic Woodpecker, and apparently the first observation of this woodpecker preying on another vertebrate. Thus, this account adds to the few reports of vertebrate predation by woodpeckers, other than eating bird eggs or nestlings.

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Male Brown-headed Cowbird Attacks and Kills a Nestling

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ABSTRACT.—I observed a male Brown-headed Cowbird (*Molothrus ater*) attack and kill a nestling of an unidentified passerine in a grassland field in Day County, South Dakota, in June 2000. The killing or removal of nestlings by female cowbirds has been reported by others, but this behavior has not been documented previously in male cowbirds. *Received 8 October 2002, accepted 3 March 2003.*

Female Brown-headed Cowbirds (*Molothrus ater*) often remove and sometimes eat host eggs (e.g., Scott et al. 1992). Female cowbirds have been observed attacking, removing, or killing nestlings (Du Bois 1956, Tate 1967, Beane and Alford 1990, Scott and McKinney 1994, Sheppard 1996), and recent technological advances in videography have provided evidence that this behavior may be more common than previously believed (Averill-Murray et al. 1999, Elliott 1999, Thompson et al. 1999, Pietz and Granfors 2000, Granfors et al. 2001, Stake and Cavanagh 2001). In some cases, female cowbirds have been observed destroying or removing entire host clutches or broods (e.g., Beane and Alford 1990, Scott and McKinney 1994, Elliott 1999, Granfors et al. 2001, Stake and Cavanagh 2001, pers. obs.).

Observations of male cowbirds exhibiting interest in nests or nest contents are uncommon (Sealy 1994), although males occasionally are observed in the vicinity of nests with females (Du Bois 1956, Mengel and Jenkinson 1970, Strausberger 1998). Friedmann (1963) described two male and three female cowbirds destroying a Chipping Sparrow (*Spizella passerina*) nest several days after two cowbird eggs had disappeared from the nest ("mafia effect"; Soler et al. 1995). Sealy (1994) reported one instance of a male cowbird removing an egg from an Eastern Kingbird (*Tyrannus tyrannus*) nest. E. Greene (pers. comm.) videotaped male cowbirds removing and consuming eggs from both artificial nests and Lazuli Bunting (*Passerina amoena*) nests in Montana. Despite these reports, male cowbirds have not previously been observed removing or killing nestlings. Here, I report my observations of a male cowbird attacking and killing a nestling in northeastern South Dakota.

On 16 June 2000 at 05:23 CST, while conducting a breeding bird survey in an idle Conservation Reserve Program grassland field (97° 45′ N, 45° 19′ W) in Day County, South Dakota, I observed a female and a male Brown-headed Cowbird flying about 0.5 m above the vegetation. The male cowbird was carrying a nestling of an unknown passerine species grasped by the neck in his bill. The nestling was flailing its legs, wings, and head, and opening its bill. A male Red-winged Blackbird (*Agelaius phoeniceus*) briefly pursued the cowbirds as they flew over the blackbird's song perch. The male cowbird alighted

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on a wooden fencepost at the edge of the field (about 25 m from my observation point) and dropped the still active nestling onto the fencepost; the female cowbird landed on a barbed wire strand near the male. While holding the nestling down with its right foot, the male cowbird repeatedly pecked the nestling's head until the nestling was motionless and bloody. The male cowbird then flew off with the limp nestling in its bill and dropped it in a nearby pasture, about 100 m from the fencepost. The female cowbird departed with the male cowbird. Although my presence may have influenced the cowbird's behavior, there was no indication that the male intended to consume the nestling. Upon searching the pasture, I was unable to locate the discarded nestling in the dense vegetation.

The species of nestling was not obvious, but it appeared to be that of a larger passerine (cowbird-sized or larger), based on its size and age (i.e., recently hatched, largely naked, sparse light gray down on head, eyes closed). Several passerine species were recorded during the breeding bird survey in the vicinity of the observation, including Red-winged Blackbird, Western Meadowlark (*Sturnella neglecta*), and Bobolink (*Dolichonyx oryzivorus*). About 33% of passerine nests ($n = 143$) found incidentally during bird surveys in grassland fields in this county between 1990 and 2002 were parasitized by cowbirds (unpubl. data).

Although I did not observe the male cowbird at a nest, the fact that the nestling was very young and still alive at the beginning of my observation suggests that it was removed from a nest recently by the male cowbird or possibly by a female cowbird. There is increasing evidence that female cowbirds may destroy or remove the contents of nests that they do not intend to parasitize (Arcese et al. 1996, Granfors et al. 2001), but the motivation of such predatory behavior in cowbirds remains speculative. A number of researchers have suggested that consumption of nestlings is not the primary reason for cowbirds removing nestlings from a nest (Scott et al. 1992, Sealy 1994, Ortega 1998, Granfors et al. 2001). Arcese and coworkers (1992, 1996) speculated that cowbirds will destroy nest contents late in the nesting cycle to induce hosts to renest, thus enabling the cowbird to synchronize their egg laying with that of the renesting host. Cowbirds also may disrupt nests in the vicinity of their hosts' nests to reduce competition for the cowbird nestling's food (Granfors et al. 2001) or to reduce competition among conspecifics (Laskey 1950).

Elliott (1999) suggested that infanticide rather than predation may be a more appropriate term to characterize the cowbird's behavior of removing nestlings from nests, because cowbirds do not eat the nestlings and because cowbird fecundity may be enhanced by increased breeding opportunities from the renesting hosts. Regardless of the intent of this male's behavior or the terminology used to describe it, the killing or removal of nestlings appears to be rare among male cowbirds.

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New Record of Shiny Cowbird (*Molothrus bonariensis*) Parasitism of Black-chinned Siskins (*Carduelis barbata*)

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ABSTRACT.—I present the second record of Shiny Cowbird (*Molothrus bonariensis*) parasitism of the Black-chinned Siskin (*Carduelis barbata*). The last recorded observation was in 1929. This also represents the northernmost nesting record of the Black-chinned Siskin. *Received 6 August 2002, accepted 23 February 2003.*

Brood parasitism is a breeding strategy in which parasites lay eggs in the nests of other species (hosts) which incubate eggs and provide parental care to the offspring. The Shiny Cowbird (*Molothrus bonariensis*) is a generalist, obligate, brood parasite. The Black-chinned Siskin (*Carduelis barbata*) was reported to be a host of Shiny Cowbirds in the Cape San Antonio, Buenos Aires province, Argentina (Gibson in Friedmann 1929). This record has been cited in several works (Friedmann 1963, Friedmann and Kiff 1985, Ortega 1998) but no new records have been reported. Here I present new information related to Shiny Cowbirds parasitizing Black-chinned Siskins.

The Black-chinned Siskin occurs only in South America. The known distribution of this species includes Chile, except for the North Atacama Region, and Argentina, from the provinces of Neuquen and Rio Negro to Tierra del Fuego (Ridgely and Tudor 1989). Shiny Cowbirds historically were confined to grasslands and open woods of South America (Friedmann 1929) and, more recently, expanded their range into areas that have been transformed for agriculture or animal husbandry (Post et al. 1990). Presently, Shiny Cowbirds occur in the central and southern areas of South America, excluding the High Andes, south of Patagonia, and unexploited areas of Amazonia (Ridgely and Tudor 1989).

On 25 October 1999, I found a Black-chinned Siskin nest containing one host egg and one Shiny Cowbird egg in San Carlos, Mendoza province, Argentina (33° 44′ S, 69°

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07′ W). The nest was located in a poplar (*Populus* sp.) inside a small, open poplar wood (<1 ha). During a second visit 2 days later, I found the nest empty, probably depredated. Two Black-chinned Siskin adults, a male and a female, were perched near the nest and gave alarm vocalizations.

One of the main costs suffered by Shiny Cowbird's hosts is the loss of eggs through punctures made by the parasite (Hoy and Ottow 1964; Mermoz and Reboreda 1998; Massoni and Reboreda 1998, 2002). In addition, parasitic eggs can reduce the hatchability of host eggs (Blankespoor et al. 1982, Petit 1991), and parasite chicks can outcompete host chicks for food (Post and Wiley 1977). As the eggs I discovered did not hatch, I do not know if the Black-chinned Siskins would have incubated the cowbird's egg and raised its young, or if their own young would have hatched or fledged.

This observation also is significant because San Carlos is located more than 500 km north of the known breeding range of the Black-chinned Siskin. As Shiny Cowbirds are expanding their range into new areas, Black-chinned Siskins may become more frequently parasitized. Further studies are needed to determine which species are being parasitized in regions newly occupied by cowbirds.

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Parental Care in the Great Kiskadee

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ABSTRACT.—We studied parental care in the Great Kiskadee (*Pitangus sulphuratus*) in a suburban residential area in Buenos Aires Province, Argentina, from September through December, 1998. Our data suggest that the dominant breeding system of the Great Kiskadees on our study site is social monogamy. Both male and female were involved in territory defense, nest building, and feeding the young. The female alone incubated the eggs and brooded the nestlings. Male and female visitation rates to the nest during the nestling period were similar. *Received 18 October 2002, accepted 10 March 2003.*

Parental investment is any form of parental behavior that increases the chances of offspring survival to independence (Clutton-Brock 1991). In birds, it may range from nest site selection and territorial defense, to the provision of food to nestlings and fledglings.

Oring (1982) suggested that oviparity and the appearance of endothermy in the Class Aves might have promoted the need for biparental care, as both factors require a large parental investment, leading to the advent of social monogamy as the most common mating system of the group (Lack 1968). However, the degree of sexual dimorphism, as a consequence of sexual selection acting on the species, greatly influences the relative parental contributions of each member of the pair. Thus, the mating system of any given species usually is intimately tied to the degree of sexual selection of that species, and to the parental roles during the nesting period and territory defense (Ligon 1999, Stutchbury and Morton 2001).

The dominant social mating system of tyrant flycatchers (Tyrannidae) is monogamy, with females generally being in charge of nest construction and incubation, and biparental attention during the nestling period (Skutch 1960, Verner and Willson 1969). The Great Kiskadee (*Pitangus sulphuratus*) is a widespread monomorphic flycatcher that inhabits semi-open habitats from the southern United States (Texas) to southern Argentina (Ridgely and Tudor 1994). Although it is an abundant species throughout its range, its parental behavior is poorly known. Kiskadees are believed to be socially monogamous, retaining their territories year round (Brush and Fitzpatrick 2002). Typically, they build a dome-shaped nest with a side entrance, constructed of grasses and other fine material (Baicich and Harrison 1997), but open cup nests also have been reported (Smith 1962, Sick 1985). The nest usually is located on an exposed tree branch (Sick 1985), with some nests also being found in cavities or recesses (Zuberbhuler 1971, Haverschmidt 1974, Lago-Paiva 1996). Here we present data on the parental roles of the Great Kiskadee during the breeding season in a suburban area in Buenos Aires Province, Argentina.

METHODS

From October to December, 1998, we studied parental care during the breeding cycle of the Great Kiskadee in a suburban area near the town of Escobar (34° 17′ S, 48° 45′ W), Buenos Aires Province, Argentina. The area is a 10-ha mosaic of parks and lawns, with a considerable number of introduced trees (*Juniperus* spp., *Cupressuss* spp., *Libocedrus* spp., *Eucalyptus* spp.), and a small number of native trees (*Celtis tala*, *Acacia aroma*).

During September 1998, we captured a total of eight kiskadees using mist nets. Each individual was given a unique color band combination. We found 11 nests using behavioral cues and systematic searching. We determined the adult activity during each stage of the nesting cycle by focal sampling. We monitored each nest for 30 min during building, 60 min during incubation, and 60 min during the nestling period, twice for each period (during the morning and afternoon). Adults were easy to observe during incubation and while feeding nestlings, allowing us to identify them by their color band combinations. Because nests were too high to access, we could not control

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for age and number of nestlings when assessing male and female feeding rates, but we were able to compare male and female activity rates for each nest. Since individuals were recaptured with mist nets during the breeding cycle, we were able to sex birds by looking at brood patch development or presence of a cloacal protuberance. We used this morphological sex determination to establish male and female parental roles at nests. We made all our observations from a distance of approximately 20 m with 10 × 42 binoculars.

We compared male and female parental contributions using a Wilcoxon matched-pairs test (Siegel and Castellan 1988, Lehner 1996).

RESULTS AND DISCUSSION

We monitored a total of 11 nests during building. All nests were domed with side entrances, constructed of dry grass, and usually placed 2–10 m above ground. At nests in which we could identify at least one member of the pair ($n = 6$), two adults were seen building. In the five remaining nests, we observed both individuals on several occasions taking material simultaneously to the nest and going inside to build the cup or the dome. Although nests from the previous year lasted long enough that they were still present at the beginning of the breeding season, they were never re-used by kiskadees. However, in five instances we saw birds re-using material from old kiskadee nests for building new nests. In one instance we observed a pair of kiskadees taking material from a nest of a White-winged Becard (*Pachyramphus polychopterus*), which was being built 7 m away from their nest. The becards finally deserted the nest and the kiskadees used most of the material. On two other occasions we observed kiskadees stealing material from active nests of neighboring kiskadee pairs that also were building. These events led to chases and fights between adults, but not to desertion. Stealing nest material seems to be a common strategy for these birds and has been observed in other locations (Brush and Fitzpatrick 2002).

We monitored incubation at four nests with at least one adult banded, and two nests with both adults banded. At all nests we monitored, only the females incubated. We observed a total of 25 incubation on-bouts and 14 off-bouts. The longest on-bout was 45 min, while the shortest was 7 min (mean = 16.48 min ± 1.64 SE). Off-bouts ranged from 2–13 min (mean = 6.28 min ± 0.87 SE). During the females' off-bouts, males usually perched 2–6 m from the nest. This behavior could be related to nest defense against predators, brood parasites, or other kiskadees, which might steal material from the nest or prey on the eggs or nestlings (Gorena 1995, Robinson 1997). On seven occasions we observed males from four different pairs chasing other kiskadees from the nest vicinity during the incubation stage.

During the nestling period we monitored five nests, two nests with both adults banded and three nests with one adult banded. We observed a total of 86 food-provisioning trips to the nestlings. We found no significant differences between the visitation rates of males and females (means of 9.40 trips/h ± 1.29 SE and 7.80 trips/h ± 1.83 SE, respectively; $Z = 0.730$, $P = 0.47$).

We observed 10 brooding bouts, ranging from 9–54 min (mean = 22.5 min ± 5.33 SE). Only the females brooded young. We never observed males feeding nestlings while the female was brooding; males instead perched on a nearby branch and delivered food to the nestlings after the female left the nest.

During the breeding season, we observed six territorial fights; four involved both members of the pair. At our field site, kiskadees were aggressive to other adults and defended a territory year round. Both members of the pair chased other kiskadees immediately out of the territory. Kiskadees are known to attack and destroy each other's nests (R. Fraga pers. comm.). Fights included male-female dueting, bill snapping, exposing the semiconcealed yellow coronal patch, and aerial chases.

We never observed a banded male attending more than one nest, and we never saw more than two birds attending the same nest. Thus, we suggest that the breeding system of the Great Kiskadee in our study site was social monogamy. This behavioral system closely resembles some of the systems present in the Neotropics, in which males and females have stable pair bonds, share most of the parental care duties, and defend their territories year round (Stutchbury and Morton 2001). Social monogamy in kiskadees has been reported previously in other populations (Gorena 1995, Robinson 1997, Brush and Fitzpatrick 2002).

Although male kiskadees do not incubate, they certainly guard nests during incubation. Unlike most of the tyrant flycatchers, they actively participate in nest building (Skutch 1960), and their parental care duties are consistent with that expected of a monomorphic, monogamous species (Verner and Willson 1969). Finally, our conclusions should be taken with caution since they are based on a small sample size gathered during a single breeding season. Future research is needed for a better understanding of the parental roles and genetic, as well as social, mating system in the Great Kiskadee.

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Ornithological Literature

Edited by Mary Gustafson

RATITES AND TINAMOUS: Tinamidae, Rheidae, Dromaiidae, Casuariidae, Apterygidae, Struthionidae. By S. J. J. F. Davies. Oxford Univ. Press, Oxford. 2002: 310 pp., 12 color plates by Michael J. Bamford, numerous range maps and line drawings by Danika Loomes. ISBN 0-19-854996-2. $85 (cloth).—This ninth volume in the Oxford Univ. Press series *Bird families of the world* treats eight families of birds, the six mentioned in the title plus the extinct families of moas (Dinornithidae) and elephant birds (Aepyornithidae). The author follows the classification of Bock and Buhler (Bonn 1988, pp 31–36 *in* Proc. Int. 100. DO-G Meeting, Current Topics in Avian Biology) and thus includes the eight families in the Order Struthioniformes, with the tinamous (Tinamidae) and rheas (Rheidae) grouped together in one superfamily, the emus (Dromaiidae) cassowaries (Casuaridae), moas, and kiwis (Apterygidae) in another, and the ostrich (Struthionidae) and elephant bird in a third. All but the timamous are (or were) relatively large, flightless birds.

The book is divided into two parts. The first part consists of a historical prologue that recounts early references to the elephant birds and moas, followed by seven general chapters. The second part consists of family, genus, and species accounts. Fifty-seven species of living ratites and tinamous are treated, with accounts ranging from about 1–12 pages, reflecting the widely differing information base among species. Chapter 1 is a rather complex discussion of the evolution of the ratites that includes discussion of osteology, feathers, oil gland, musculature, pores in eggshells, fossils, and a host of other characters. The various conflicting opinions about taxonomic status of the families and their interrelationships are discussed, along with questions relating to monophyletic or polyphyletic origin of the group, whether the ratites are primitive or derived from flying ancestors, and how the various groups achieved their present distribution. Experts still disagree on the answers to many of these questions. Finally, the author addresses the question of why the elephant birds, moas, and two species of small emus became extinct. The second chapter, "Design Concepts: Birds That Don't Fly," includes discussion of the advantages and disadvantages of increased size, ratite physiology, adaptations to bipedal lifestyles, and sensing and avoiding potential danger. Chapter 3 deals with feeding ecology; Chapter 4 is titled "The Consequences of Nomadism, Non-breeding Behaviour and Biology"; Chapter 5 covers mating systems and breeding biology; Chapter 6 focuses on human interactions, including mythology, hunting, and farming; and Chapter 7 gives a brief look into the future of ratites and tinamous.

The species accounts begin with a nomenclature synopsis, then a description of the adult male and female, immature and downy young, along with subspecies information, molt and measurement; field characters (highlighting differences from similar species); voice; range, habitat and status (including a range map that includes any subspecies); feeding and general habits; displays and breeding behavior (courtship); and breeding and life cycle (post courtship). Voice is presented by description and mnemonics rather than by sonagrams, although a few representative sonagrams for the various families are presented in Chapter 4. Each species is figured on one of the color plates, accompanied by a brief description on the facing page. Most of the tinamous (47 species) are nearly monomorphic, so only a single image is presented, although in a few cases both adult male and female are presented and several distinctive subspecies are portrayed. The plates are of generally good quality, although a bit two-dimensional to my eyes, and have sufficient images of young and male and female plumages in dimorphic species. Following the species accounts, Appendix 1 presents alternative names for species, and a second appendix gives a synopsis of the classification adopted in this book. The alternative names appendix is short, and I think the names would have been better included in the species accounts.

The References section contains nearly 400 entries.

I have few faults to find with this book. Like all of the books of this series, it is generally well written and thorough, although the complex nature of the arguments over evolution and taxonomy in this group of families makes for some rough going. There are a few typos, e.g., in Plate 6 the 260–280 cm size listed for the White-bellied Nothura (*Nothura boraquira*) would make it a very large bird indeed! In one place "interspecific" should have been "intraspecific." The use of bantams for size comparisons with the tinamous is inconsistent, e.g., Plates 6 and 7: "31–35 cm; size of a small bantam"; "25–29 cm; size of a bantam"; "39–42 cm; size of a bantam"; and "39–42 cm; The size of a large bantam." I did not find these kinds of comparisons very helpful. I also found the font too fine for easy reading. These minor problems should not detract from the overall excellence of the book and the series. The book should have heuristic value, as what is not known about many of these species is remarkable. For example, for Bartlett's Tinamou (*Crypturellus bartletti*), which is regarded as common in parts of Peru, in the Moult section is the entry "no information available," in Feeding and General Habits "no information is available about its feeding habits or diet"; in Display and Breeding Behaviour "No information available," and under Breeding and Life-style "No information available." This book should be part of every academic library and should be welcomed by anyone with an interest in this fascinating group of birds.—WILLIAM E. DAVIS, JR.

NIGHTJARS AND THEIR ALLIES. By David T. Holyoak, illustrated by Martin Woodcock. From the series *Bird families of the world.* Oxford Univ. Press, Oxford. 2001: 774 pp., 23 color plates, numerous halftones, line drawings, and distribution maps. ISBN 0-19-854987-3. $85.00 (cloth).—This is a very interesting book on the 118 species of oilbirds (Steatornithidae), frogmouths (Podargidae), potoos (Nyctibiidae), owlet-nightjars (Aegothelidae), and nighthawks and nightjars (Caprimulgidae). It was written in a manner that makes it useful to both the professional ornithologist and the casual birdwatcher. The author faces tough competition by two other books published in recent years, Cleere and Nurney (1998, Nightjars: a guide to nightjars and related nightbirds, Pica Press, Sussex, United Kingdom) and del Hoyo et al. (1999: 241–386, Handbook of the birds of the world, vol. 5: barn owls to hummingbirds, Lynx Edicions, Barcelona, Spain) that covered the same families. This competition requires a comparison of the three books, even though this review is focused on the newest of the three.

The first parts of book, preceding the species accounts, consists of sections dealing with the layout of the book (Abbreviations, Plan of the Book, and Topography of a Nightjar), and chapters titled Introduction to the Caprimulgiformes (which includes human superstitious beliefs); Evolution and Classification; Speciation and Biogeography; Habitats, Migration, and Hibernation; Food and Feeding Ecology; Nocturnal Signaling; Breeding Biology; and Molt.

The species accounts vary in length from just under two pages for little-studied (mostly equatorial) species to 16 pages for better-studied species. Each account consists of plumage descriptions (including molts, bare parts, measurements, and geographical variation), range and status, habitat, food and feeding, behavior, voice, breeding, field characters, conservation, common names in a select number of languages, and references. The information presented on conservation is particularly important, given the rapid changes the world is undergoing.

I was struck by how little is known about this family of nocturnal and cryptically colored birds. However, the author attempted to gather every little bit of information published worldwide. The species accounts are extensive and detailed, and are presented in a very interesting manner. A comparison of text length illustrates how much detail Holyoak presents: the species account for the Common Nighthawk (*Chordeiles minor*) takes up 16 pages in *Nightjars and their allies* compared to only 5 pages in *Guide to nightjars and related nightbirds.*

The plates are of great artistic value, and they represent the perched bird well. I was

disappointed that only 4 of the 118 species were depicted in flight in color drawings. Some of the other species accounts include black and white drawings showing the diagnostic markings mentioned in the Field Characters section. I expect these characters will be of little value to the reader who wants to compare the gestalt of a bird observed in the field with the drawings in the book. A strength of *Guide to nightjars and related nightbirds* is that all species are illustrated both perched and in flight.

In regard to the usefulness of *Nightjars and their allies* for scientific research, I commend the authors on the exhaustive bibliography, which spans 64 pages, compared to 15 in *Guide to nightjars and related nightbirds* or the limited bibliography of the *Handbook of the birds of the world.* I also found the detailed chapters (a total of 92 pages) at the beginning of *Nightjars and their allies* to be interesting, easily read, and very informative. The author presents not only what is known about each species, but also what remains to be studied in the future.

I found several substantial differences among the books. The font used for *Nightjars and their allies* is larger than that of the other two, which makes it easier to read at length. The maps also are larger, and the greater detail allows one to delineate areas based on geopolitical boundaries. Perhaps the biggest difference among the three books, other than price, is their weights; my copies of *Guide to nightjars and related nightbirds* weighed 950 g, *Nightjars and their allies* 1,900 g, and *Handbook* 3,950 g. Clearly, one is suited for a field guide, another for the bookshelf, and the heaviest for the coffee table. I will be putting *Nightjars and their allies* in my backpack the next time I go Nighthawking.—REUVEN YOSEF.

OISEAUX D'AFRIQUE 1. (AFRICAN BIRD SOUNDS 1). By Claude Chappuis. Societe d'Etudes Ornithologiques de France, Paris. 2000: four audio compact disks and a 68-page booklet. 380 francs—The vocalizations of 423 African birds are included on this four-CD compilation produced by the French Ornithological Society in collaboration with the British Library National Sound Archive (London). Volume 1 represents the first part of a series dedicated to the study of the birds of north, west, and central Africa and neighboring islands, i.e., birds of the Sahara, Maghreb, Madera, Canaria and Cape Verde.

The booklet, in French and English, is easy to use and instructive, and has the following sections: Conception; History; Content, Systematic or Evolutionary Problems; Use of the Work, Definitions and Conventions; Technical Characteristics; and Acknowledgments. Information for each species includes location on the CD, scientific name, common name in English and French, status, type of call, location of the recording, and recording length. A concluding, cautionary paragraph reminds the user that misuse of the recorded vocalizations could be harmful to some birds, especially endangered species.

The four CDs include vocalizations of 423 of the 425 species reported for the region. They are of high quality and will help the user identify vocalizations to the correct species. This is an excellent product and will be useful to anyone interested in the vocalizations of breeding or migratory birds of North and Central Africa.—REUVEN YOSEF.

MICE IN THE FREEZER, OWLS ON THE PORCH: THE LIVES OF NATURALISTS FREDERICK AND FRANCES HAMERSTROM. By Helen McGavran Corneli. The Univ. of Wisconsin Press, Madison. 2002: 328 pp., 40 black-and-white photographs. ISBN 0-299-18090-5. $29.95 (cloth).—Friends, colleagues and admirers of the Hamerstroms have been awaiting this biography for years. Most intimates of the Hamerstroms expected the book to be completed and published only after the death of Fran Hamerstrom, for reasons that become understandable to readers of this book. One way of describing this biography of Frederick and Frances Hamerstrom would be to call it a love story, set in a background of wildlife research and conservation. Family friend Adalbert Ebner, quoted in the book, called the Hamerstrom marriage "perfection." Corneli quoted further the interpretation of Adalbert Egner on the relationship and life of the Hamerstroms: "You work together, your work is common, your love is

common, you have fun together, for me you are the perfection."

Helen Corneli, the author of this Hamerstrom biography, was a long time neighbor of the Hamerstroms in rural Wisconsin, and she freely concedes that her perspective as a neighbor influenced her writing of the book, so that a much different biography might have been written by a professional colleague, a relative, or some other author with a different background.

Corneli's great contribution to the biography and understanding of the lives of the Hamerstroms is her great depth of research: contacting old associates, family members, reviewing records, and digging deeply into the thoughts of those who worked, studied, and interacted with the Hamerstroms over many years. Corneli retraces the childhood of Fran, and provides some context and clarity for the benefit of readers of Fran's several autobiographies, which tended to emphasize only negative aspects of both of Fran's parents and her home life as a child. By interviewing Fran's surviving brother, Putnam Flint, the reader comes to appreciate that perhaps the family environment in the Flint home was not so awful as Fran had described, and their parents were perhaps more normal, loving, and kind than some of Fran's own writings would tend to indicate. Frederick's childhood could not be as well documented as that of Fran, due to lack of surviving records.

The marriage, life as young married adults, and prime career of the Hamerstroms are well documented in this book. The Hamerstroms came into their own in a different age, even in the history of wildlife research and conservation. Women were made to feel distinctly unwelcome in the "game management" field, and so Fran and Frederick had to persevere. The Hamerstroms encountered numerous hardships and challenges, but relied upon their own incredible stamina, mutual love, and dedication and determination to succeed in their careers.

One of the fascinating historical episodes that was well documented in this book was the effort to assist starving German ornithologists after the Second World War. Along with Doctor and Mrs. Ernst Mayr of Harvard Univ. and a number of other colleagues, the Hamerstroms played an integral role in cataloguing the needs of European colleagues, right down to shoe sizes, and then collecting desperately needed food and clothing, thus not only making life more bearable for foreign colleagues in deep distress, but also in forging international links of friendship and collegiality that became a hallmark of Hamerstrom life for decades to come.

Much about the lives and philosophy and careers of the Hamerstroms was unique. This book describes many details, such as inviting literally thousands of strangers into the Hamerstrom home to observe and record data on the behaviors of Greater Prairie Chickens (*Tympanuchus cupido*). The lives of the Hamerstrom children were atypical and this book describes some of the goings-on that made life in the Hamerstrom household quite unusual, and perhaps traumatic at times for the Hamerstrom children.

Many famous and extraordinary people were integral parts of the lives of the Hamerstroms, including Nobel Prize winning scientists, famous ornithologists, and notable people from many walks of life. The philosophies and impacts of the Hamerstroms are well documented, such as their passion for public service and adventure. The lives of the Hamerstroms were heavily accentuated by both.

If there is one disappointment with this book, it is that the detailed attention to careers and activities is focused primarily on the early years and prime careers of Frederick and Fran, time periods that were covered best by Fran's own autobiographical works. As a result, relatively little detail is given to the raptor research of the Hamerstroms, or stories of the formation of groups the Hamerstroms helped organize and support, such as the Raptor Research Foundation and the North American Falconers Association. There are brief summaries of some of those activities, but little of the rich detail seen in descriptions of the earlier phases of the lives of the Hamerstroms.

Certainly, the lives of Frederick and Frances Hamerstrom were so rich and colorful and impacting on their fields of interest that perhaps several volumes could be written. An amazing evidence of the impacts of the Hamerstroms in the field of wildlife research and management is that two completely separate wildlife research organizations representing very different taxa, the Prairie Grouse Tech-

nical Council and the Raptor Research Foundation, both have named major lifetime achievement awards after the Hamerstroms.

Countless citizens and professionals have been influenced and inspired by the lives, the work, and personal interactions with Frederick and Frances Hamerstrom. Helen Corneli, their old neighbor, has done a great service in documenting fascinating aspects of their lives. Anyone interested in wildlife, conservation, grouse, raptors, or nature itself will find joy and inspiration in this book. Friends and colleagues, gabboons, and other intimates of the Hamerstroms will find great joy in the recollections and deep meaning by relating the events recorded in this book with their own experiences.—STAN MOORE.

BIRDS OF THE SASKATOON AREA. Edited by A. L. Leighton, J. Hay, C. S. Houston, J. F. Roy, S. Shadick, and M. Gilliland. Special Publications No. 5, Saskatchewan Natural History Society. 2002: 345 pp., 14 maps, many color photographs of habitat, 40 line drawings of birds. $39.00 Cdn plus postage (Paper, spiral bound).—Because the Saskatoon area of southcentral Saskatchewan consists largely of prairie grasslands with a fringe of aspen forest in the north and represents only a small fraction of a huge and floristically diverse Province, some might think that *Birds of the Saskatoon area* might be of only local interest. However, the area under consideration is enormous (11,000 km^2) and information is presented in the context of the entire Province. Accordingly, this book, along with the recent *Atlas of Saskatchewan birds* (1996, Environment Canada, Nature Saskatchewan), provides a good index to the status of birdlife over a much wider region.

Prepared by 77 volunteer contributors and six editors—the core of the Saskatchewan ornithological community—this publication is aimed at a broad audience and will be useful to local novice naturalists as well as to professional biologists and managers. Its wide range of information includes the history of local ornithology, geology and geomorphology, plant life and avian associations, how to watch birds, directions and maps of local birding hot spots (this section is so complete that it could double as an ABA Guide), and even the dimensions of nest boxes for local species. The heart of the book is the 341 species accounts (nearly 250 pages). These are nicely written essays with information on basic biology, status, migration dates, behavior, habits, and identification. Not infrequently, these accounts include information that is too detailed for general readership, such as the street address for a Pine Siskin (*Carduelis pinus*) nest, the fact that an Orchard Oriole (*Icterus spurius*) appeared on Vic Harper's farm, or the full names of everyone that observed a rarity. However, a major goal of the book is to stimulate local interest in birds and their conservation, and this can require a little honey. The reader also will find comments that will elicit some reflection, such as the intimation that Ovenbirds (*Seiurus aurocapillus*) may be especially susceptible to transmission line kills. Books such as this offer a good outlet for ideas or observations that are too brief and anecdotal for formal publications but are based on the impressions of serious observers.

A major contribution is the summary information on the number of birds banded in the Saskatoon area (73,619 of 171 species, including 6,208 game birds), of which nearly 42,000 were tagged by the indefatigable C. S. Houston. The data are presented in enough detail that specialists will be able to determine if further analysis might be fruitful. It is disconcerting, however, to realize how few banded birds are recovered, even among species that frequent feeders (e.g., only 3 of 2,600 Dark-eyed Juncos (*Junco hyemalis*), 1 of 1,900 White-throated Sparrows (*Zonotrichia albicollis*). It makes one wonder where all these Saskatchewan birds go. The species with the most numerous recoveries (1,510) is the delectable Mallard (*Anas platyrhynchos*). The most interesting recovery was a Pectoral Sandpiper (*Calidris melanotos*) caught in autumn and recovered on (ostensibly) its breeding grounds in northern Siberia. The book also includes a table summarizing "statistically significant" population changes as measured by the Breeding Bird Survey, by decade, since 1971. These are presented at face value, without noting that BBS methods are not applicable to many species, particularly nonpasserines.

The Saskatchewan Natural History Society has had a long record of publishing contributions to the ornithology of the Province. This "unusually complete regional study" continues that tradition. Along with other publications of the SNHS, it provides an important baseline for future work. For someone considering writing a regional guide, this one may provide a good template.—J. R. JEHL, JR.

Announcements

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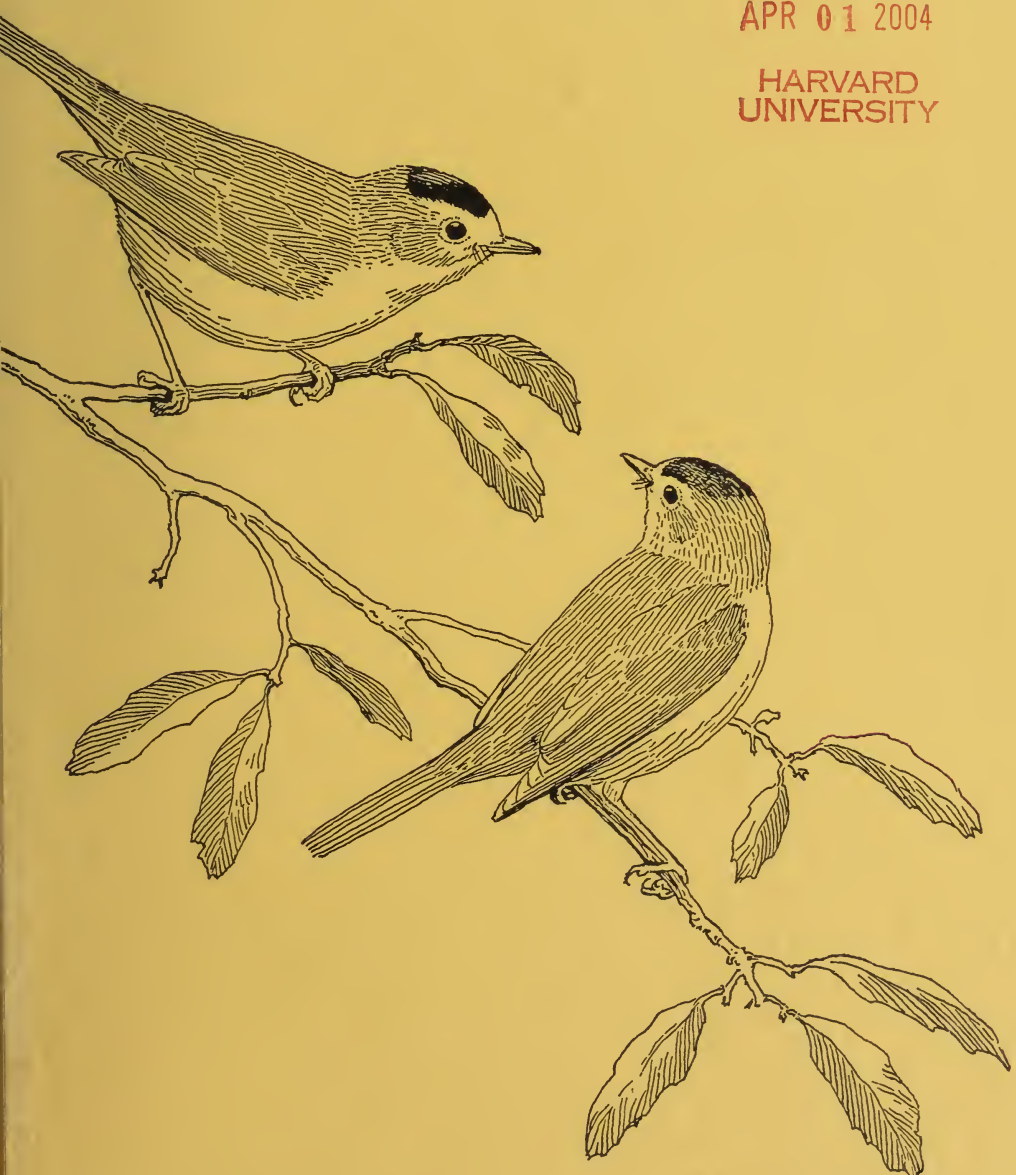

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FRONTISPIECE. Young Cooper's Hawk (*Accipiter cooperii*). Although eye color of first-year birds throughout North America begins as yellow and tends to darken to orange or strikingly red, due to individual variation, eye color is not a reliable indicator of age nor does it appear to function as a sexual trait in assortative mating. Painting (acrylic on compressed hardboard) by Barry Kent MacKay.

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COMPARATIVE RELATIONSHIPS AMONG EYE COLOR, AGE, AND SEX IN THREE NORTH AMERICAN POPULATIONS OF COOPER'S HAWKS

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ABSTRACT.—Although adult plumage in Cooper's Hawks (*Accipiter cooperii*) exhibits little or no sexual dichromatism, iris color reportedly changes from yellow or light orange in younger birds to shades of orange or red in older birds, especially in males. However, there is little quantitative data on this phenomenon. It has been suggested that male eye color may serve as a signal of age and hence reproductive fitness and thus offer a basis for nonrandom mating in Cooper's Hawks. In this study we examine the relationships between eye color and age, sex, and reproductive output for Cooper's Hawks in two breeding populations in British Columbia and North Dakota, 1999–2002, and compare these results to those previously published for a breeding population in Wisconsin, 1980–1995. Cooper's Hawks in British Columbia and North Dakota appear to acquire darker orange or red irides more frequently and more quickly than their counterparts at known and relative ages in Wisconsin. Females in all study sites are slower and less likely than males to acquire the darkest eye colors. Eye color is not a reliable predictor of age in individual male and female Cooper's Hawks, for researchers and perhaps for the birds themselves, because individual hawks of a given eye color displayed variation in known and relative ages in British Columbia and Wisconsin. There was no significant relationship between the eye color of males and their brood sizes in any of these three populations, and therefore no discernable support for the premise that male eye color *per se* signals male fitness, or functions as a sexual trait for assortative mating in this species. *Received 20 January 2003, accepted 3 June 2003.*

In the Cooper's Hawk (*Accipiter cooperii*), a species with little or no sexual dichromatism in adult plumage (Rosenfield and Bielefeldt 1993), iris color shows an age dependent relationship, especially in males, with irides typically changing from yellow or light orange in younger birds to shades of orange or red in older birds (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). Other researchers, although lacking multiyear data on eye color of individually marked birds of known age, have postulated that eye color may be a characteristic (Snyder and Snyder 1974) or one of a suite of characteristics (Boal 2001) that might signal reproductive fitness and offer the opportunity for assortative mating, but we found no correlation between male eye color and clutch or brood sizes as indices of fitness in a population in Wisconsin (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). However, the relationships between eye color and

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TABLE 1. Iris color of relative-age[a] Cooper's Hawks breeding in British Columbia during 1999–2002, and mean eye color scores (in parentheses) for corresponding relative-age birds in Wisconsin, 1980–95.[b]

	Eye color categories						
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red	*n*	Mean eye color score
Males							
ASY	0	0	7	7	11	25	4.2 (3.6)
A3Y	0	0	0	3	4	7	4.6 (3.7)
A4Y	0	0	0	1	3	4	4.8 (4.2)
A5Y	0	0	0	0	1	1	5.0 (4.7)
A6Y	0	0	0	0	1	1	5.0 (4.8)
A9Y	0	0	0	0	1	1	5.0 (5.0)
Females							
ASY	0	1	8	12	2	23	3.6 (2.8)
A3Y	0	0	1	6	1	8	4.0 (2.9)
A4Y	0	0	2	2	0	4	3.5 (3.1)
A5Y	0	0	1	1	0	2	3.5 (3.3)

[a] Relative-age birds are ASY (after-second-year) birds two or more years of age, and recaptures of these individuals (A3Y, A4Y, etc.) in subsequent years.

[b] Mean eye color scores for Wisconsin birds previously reported by Rosenfield and Bielefeldt (1997).

age, sex, and reproductive output are unreported for Cooper's Hawks elsewhere in eastern North America, or in western populations that are morphometrically separable from Wisconsin birds (JB, MAB, RKM, LJR, RNR, and ACS unpubl. data). Here we show that patterns of change in eye color with age and sex differ between Wisconsin birds and breeding birds in two western populations in British Columbia and North Dakota.

STUDY AREA AND METHODS

Previous results and methods in Wisconsin (44° 25′ N, 89° 30′ W), 1980–1995, are described in Rosenfield and Bielefeldt (1997). During 1999–2002 we applied the same methods at 45 nests in western North Dakota (48° 37′ N, 102° 27′ W), and at 85 nests on Vancouver Island, British Columbia (48° 27′ N, 123° 21′ W). For descriptions of western study areas see Murphy (1993) and Stewart et al. (1996). In North Dakota we trapped breeding Cooper's Hawks at nests, including 38 males and 31 females captured only once. In British Columbia we caught 47 individual males and 42 individual females and retrapped some of the same birds a total of 38 times in subsequent years; 51 captures and recaptures in British Columbia involved 43 individual breeding birds of known age originally captured as SY (second year) birds or marked as nestlings during 1995–2001. Relative-age birds of unknown age are classified as ASY (after second year) birds that are two or more years of age upon initial capture; recaptures of these individuals are designated A3Y, A4Y, etc., in subsequent years.

We designated eye color of captured hawks as yellow, light orange, orange, dark orange, or red following Rosenfield et al. (1992). We determined mean eye color scores for hawks in a relative age category through assignment of corresponding numerical scores of 1–5 for yellow through red eyes, respectively (Rosenfield et al. 1992). As in Wisconsin (Rosenfield and Bielefeldt 1997), we determined brood sizes in British Columbia and North Dakota by climbing to nests at the mid-nestling stage (about 16 days of age). We calculated probability values using SYSTAT (Wilkinson 1992) and StatXact-Turbo (Mehta and Patel 1992). Significance was accepted at $P < 0.05$.

RESULTS

On the British Columbia study area, in both sexes, iris color changed from lighter shades of yellow or orange in younger birds to darker shades of orange or red in older birds. This result held true for both relative-age and known-age birds (Tables 1, 2). Males exhibited a greater mean eye color score (i.e., darker eyes) than females of the same relative age in both British Columbia and North Dakota (Tables 1, 3). These results concur with pre-

TABLE 2. Iris color of known-age Cooper's Hawks breeding in British Columbia during 1999–2002 and in Wisconsin (in parentheses), 1980–2002.[a]

Age in years	Eye color categories				
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red
Males					
1	0 (2)	0 (8)	0 (1)	0 (0)	0 (0)
2	0 (0)	0 (3)	1 (12)	5 (2)	0 (0)
3	0 (0)	0 (2)	1 (5)	3 (3)	6 (1)
4	0 (0)	0 (0)	0 (3)	1 (3)	7 (2)
5	0 (0)	0 (0)	0 (0)	0 (2)	4 (1)
6	0 (0)	0 (0)	0 (0)	0 (1)	2 (0)
Females					
1	6 (12)	2 (2)	3 (0)	0 (0)	0 (0)
2	0 (0)	0 (2)	2 (0)	1 (0)	0 (0)
3	0 (0)	0 (1)	1 (2)	1 (0)	0 (0)
4	0 (1)	0 (0)	1 (1)	2 (0)	0 (0)
5	0 (0)	0 (1)	0 (1)	1 (0)	0 (0)
6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
7	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)

[a] Includes seven Wisconsin birds (1996–2002) that were not reported in Rosenfield and Bielefeldt (1997).

viously reported data for Cooper's Hawks in Wisconsin (Rosenfield and Bielefeldt 1997).

We assume that our samples of relative-age birds recaptured in subsequent years (Table 1) and individual ASY birds (Table 3) exhibit similar age distributions among breeding adults in mark-recapture studies in Wisconsin (Rosenfield and Bielefeldt 1997; JB, LJR, and RNR unpubl. data), in British Columbia (ACS unpubl. data), and in North Dakota (RKM unpubl. data). If so, adults of both sexes have significantly more ASY birds in darker eye color categories (dark orange and especially red) in British Columbia and North Dakota than in Wisconsin (Table 3). Proportions of dark orange and red eyes in both ASY males (83%) and ASY females (63%) were much greater in British Columbia and North Dakota than in Wisconsin (49% males, 19% females). In contrast to Wisconsin, where 24% of breeding ASY adults in combined sexes had yellow or light orange eyes, less than 2% (two individuals) had these lighter shades in British Columbia and North Dakota (Table 3).

In British Columbia, relative-age birds recaptured one or more times after initial capture (Table 1) also had predominately dark orange or red eyes in males (100%, $n = 14$ recaptures) and females (71%, $n = 14$ recaptures). Mean eye color score in both sexes increased with relative age in British Columbia and exceeded the mean score at the same relative age in Wisconsin in all but one case (an A9Y male) for both sexes (Table 1). Lack of independence among recaptures of relative-age birds prohibited inferential analysis of mean scores.

Breeding birds of known age in British Columbia appear to attain dark orange or red eyes more frequently and more rapidly than

TABLE 3. Iris color of ASY[a] Cooper's Hawks breeding in British Columbia (BC) and North Dakota (ND), 1999–2002, and Wisconsin (WI), 1980–95.[b] Percentages are in parentheses. Significant differences were found among eye color categories in ASY birds among all three study areas in males (Fisher's exact test, $P = 0.0005$) and females (Fisher's exact test, $P = 0.0005$), and between BC males and females ($P = 0.04$) and ND males and females ($P = 0.008$). No significant differences were found between eye color categories of BC and ND ASY males ($P = 0.19$) or females ($P = 0.89$).

	Eye color categories						
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red	*n*	Mean eye color score
Males							
BC	0	0	7 (28)	7 (28)	11 (44)	25	4.2
ND	0	0	4 (11)	16 (42)	18 (47)	38	4.4
WI	0	15 (11)	57 (40)	46 (32)	24 (17)	142	3.6
Females							
BC	0	1 (4)	8 (35)	12 (52)	2 (9)	23	3.6
ND	0	1 (3)	10 (32)	16 (52)	4 (13)	31	3.7
WI	9 (5)	53 (29)	87 (47)	33 (18)	2 (1)	184	2.8

[a] ASY (after-second-year) birds are two or more years of age at initial capture.
[b] Samples from Wisconsin previously reported by Rosenfield and Bielefeldt (1997).

TABLE 4. Mean brood size by eye color category for breeding male Cooper's Hawks and by age structure of mated pairs in North Dakota and British Columbia, 1999–2002. Sample sizes are in parentheses.

Mated pair age[a]	Eye color categories				
	3 Orange	4 Dark orange	5 Red	*U*	*P*
British Columbia					
Gray males mated to gray females	4.0 (6)	3.89 (9)	3.85 (20)	0.014	0.99
Gray males mated to gray or brown females	4.0 (6)	3.73 (15)	3.83 (24)	0.103	0.99
North Dakota					
Gray males mated to gray females	3.75 (4)	2.88 (17)	3.13 (16)	2.997	0.22

[a] Gray and brown birds are those individuals ≥2 years of age and one year old, respectively.

their counterparts in Wisconsin (Table 2). For example, no known-age males in British Columbia had light orange eyes at >2 years of age, but 5 (18%) of 28 males captured and recaptured in Wisconsin had light orange eyes at 2–3 years of age. In British Columbia, 79% of males captured and recaptured at age 3–6 years (n = 24) had red eyes, but only 17% of those in Wisconsin (n = 23) had red eyes. Forty-three percent of known-age males captured and recaptured in British Columbia (n = 30) acquired red eyes by ages 3–4, but only three males (6%) had red irides by these ages in Wisconsin.

In comparison to Wisconsin birds, known-age female hawks in British Columbia also appear to show quicker and more frequent changes toward darker irides (Table 2). Six (29%) of 21 females captured or recaptured in British Columbia had dark orange eyes at ages 2–7, while all of 9 females of the same age captured and recaptured in Wisconsin had eyes that were orange or lighter (Table 2).

We found no significant differences in brood sizes among male eye color categories in North Dakota in a sample composed exclusively of ASY, gray-plumaged adults (Table 4). Mean brood size did not vary by more than 0.87 nestlings among male eye color categories despite brood sizes that ranged from 1–4 young in North Dakota. There also were no significant differences in brood sizes among male eye color categories in British Columbia in gray-plumaged ASY pairs or in ASY males paired with brown-plumaged, second-year (SY) females (Table 4). Brood size in British Columbia varied from 1–5 young, but mean brood size among male eye color categories differed by only 0.15 and 0.27 nestlings in ASY-ASY and ASY-SY pairs, respectively. Because of small brood size samples in the orange eye color category in British Columbia and North Dakota, we also tested for differences in mean brood size between the dark orange and red eye color categories; we did not detect significant differences in either study area (all $P > 0.50$). As previously reported (Rosenfield and Bielefeldt 1997), mean brood (as well as clutch) sizes also failed to show significant differences among male eye color categories in Wisconsin.

DISCUSSION

We have shown that breeding Cooper's Hawks in British Columbia and North Dakota appear to acquire darker orange and red irides more frequently and more quickly than their counterparts of known and relative ages in Wisconsin. Despite these differences among three morphometrically separable populations of the species, with both British Columbia and North Dakota birds smaller than Wisconsin birds but comparable to each other in size (LJR et al. unpubl. data), similar sexual disparities in eye color persist among British Columbia, North Dakota, and Wisconsin populations. In general, females are slower and less likely than males to acquire the darkest iris colors, and some of the oldest females had not yet acquired red eyes at ages of up to A9Y (Tables 1–3; Rosenfield and Bielefeldt 1997).

It is conceivable that populations in British Columbia and North Dakota might show delayed breeding in comparison to Wisconsin birds, so that our samples of relative-age (Table 1) and ASY (Table 3) hawks in British Columbia and North Dakota might be construed to show that younger males as known-

age breeders were more numerous in Wisconsin than in British Columbia. However, even if delayed breeding were to occur in British Columbia, known-age males there acquired darker eyes more frequently and more rapidly than males of the same age in Wisconsin (Table 2). Therefore, the possibility of delayed breeding in British Columbia does not compromise our conclusion about eye color in known-age birds. We thus assume that any possible effects of delayed breeding also would have minimal effects on our conclusions regarding ASY birds in the three study populations. As in Wisconsin (Rosenfield and Bielefeldt 1997), eye color in British Columbia is not a reliable predictor of age in individual male and female hawks, for researchers and perhaps for the birds themselves, because individuals in the same eye color category displayed variation in known or relative ages (Tables 1, 2).

Because male Cooper's Hawks are the principal provider of prey to females and young during preincubation, incubation, and nestling stages (Rosenfield and Bielefeldt 1993), we have used clutch and brood sizes as indices of provisioning abilities and hence male fitness (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). Noting that male eye color darkens in older birds, Snyder and Snyder (1974: 221) suggested that darker eyes "could be a good indicator" of hunting abilities and male fitness as well as male age. However, using brood sizes as an index, we found no significant relationships between eye color in males and their brood sizes in North Dakota or British Columbia (Table 4) or Wisconsin (Rosenfield and Bielefeldt 1997), and thus no discernable support for the premise that male eye color *per se* signals male fitness.

It is possible that human perception of colors do not correspond to those of birds (Mahler and Kempenaers 2002); some species, including some raptors (Viitala et al. 1995), are sensitive to near-ultraviolet wavelengths. We are unable to dismiss that possibility in this analysis. Even so, using human perception in eye color analyses prompted by prior propositions (Snyder and Snyder 1974, Boal 2001) that assortative mating may occur on the basis of age and eye color in Cooper's Hawks, we were unable to detect any relationship between male eye color and male fitness. We have demonstrated that nonrandom mating in Cooper's Hawks in Wisconsin is related to variations in body mass and wing chord, and that such assortative mating does carry positive fitness consequences, including recruitment, for some pairs (Rosenfield and Bielefeldt 1999). If nonrandom mating on the basis of eye color were to occur in Cooper's Hawks, we could not detect selective benefits in our study of three North American populations, despite the variation in pace of eye color change and the varied proportion of darker irides among these populations. Although some studies have succeeded in discovering patterns of assortative mating using sexual traits in univariate approaches (e.g., Andersson 1982, Smith and Montgomerie 1991, Olsen et al. 1998, Rosenfield and Bielefeldt 1999, Regosin and Pruett-Jones 2001), Badyaev and Qvarnstrom (2002) have cautioned that ecological settings and behaviors in combination with single sexual traits may be involved in mate choice in birds.

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A PROBABLE GRASSHOPPER × SAVANNAH SPARROW HYBRID SINGING A SONG SPARROW SONG

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ABSTRACT.—We observed a male sparrow in May 1999 in Stow, Massachusetts, that showed hybrid characteristics resembling both Grasshopper Sparrow (*Ammodramus savannarum*) and Savannah Sparrow (*Passerculus sandwichensis*). During 1999 and 2000, this male sang a simplified Song Sparrow (*Melospiza melodia*) song. However, in 2001 it also sang a typical Savannah Sparrow song and frequently alternated between these two songs. We recorded songs and captured this individual in an area with numerous Song Sparrows and about three pairs of Savannah Sparrows. We compared mitochondrial DNA, morphological measurements, behavior, and audio spectrograms of this hybrid with similar data from Grasshopper, Savannah, and Song sparrows. Genetic analysis indicated that the hybrid's mother was almost certainly a Grasshopper Sparrow. The hybrid showed morphological traits that were within the range of both Savannah Sparrow and Song Sparrow, but generally were more consistent for Savannah Sparrow. We observed this individual frequently associating with Savannah Sparrows, attempting to copulate with a female Savannah Sparrow, carrying Savannah Sparrow fecal sacs, and feeding young Savannah Sparrows, lending additional support to Savannah Sparrow paternity. We conclude that this individual was a Grasshopper × Savannah sparrow hybrid that learned to imitate the songs of Song Sparrows at an early stage of development. Interestingly, the hybrid's exposed culmen was considerably longer than culmen measurements of any of the three species of sparrows under consideration. *Received 16 October 2002, accepted 19 May 2003.*

Approximately 10% of all bird species have been reported to produce hybrid offspring, and 8% of species in the order Passeriformes hybridize (Grant and Grant 1992). Evidence of natural hybridization can provide important insights regarding established phylogenies and can shed light on species relationships (Lewontin and Birch 1966).

We first observed a unique sparrow at Delaney Wildlife Management Area (42° 27′ N, 71° 33′ W) in Stow, Massachusetts, on 15 May 1999 that delivered a song similar to that of the Song Sparrow (*Melospiza melodia*), but that had morphological features more consistent with the Grasshopper Sparrow (*Ammodramus savannarum*) and the Savannah Sparrow (*Passerculus sandwichensis*; Fig. 1). We observed this apparent hybrid in a small, flat, open grassland of approximately 5 ha, bordered by shrubs along a stream and woodland edge.

Grasshopper Sparrows are uncommon and local in Massachusetts, with only 18 known breeding sites (Jones 2000). One to two territorial male Grasshopper Sparrows had been recorded at this site since 1993 (Jones and Vickery 1997). Savannah Sparrows are common in Massachusetts (Veit and Petersen 1993) and three to four pairs bred at this site during this period. Both species nest in grasslands, usually with sparse shrubs and weeds, and tend to avoid forested edges (Rising 1996, Vickery 1996). Song Sparrows also are common in Massachusetts and were observed regularly in the brushy habitats bordering this grassland, as well as perched on weed stalks in the grassland (ALJ pers. obs.).

There has been one report of a Grasshopper Sparrow hybridizing with a Savannah Sparrow (Dickerman 1968), but no reports of Grasshopper × Song sparrow hybrids and to our knowledge, this is the first report of a hybrid learning the song that differed from either parent. To determine the parents of this unusual, presumably hybrid sparrow, we compared mitochondrial DNA (mtDNA), morphological characteristics, behavior, and vocalizations of the hybrid with Grasshopper, Savannah, and Song sparrows.

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FIG. 1. Presumed Grasshopper × Savannah Sparrow hybrid, Stow, Massachusetts, 25 July 1999. (A) The flat-headed profile and yellow lores closely resembles the Grasshopper Sparrow, (B) the underwing and faintly streaked flank and breast are similar to the Savannah Sparrow, (C) the dark crown with a thin pale median stripe is similar to the Grasshopper Sparrow, and (D) the short tail is similar to Grasshopper and Savannah Sparrows. The very long culmen is considerably longer than Grasshopper, Savannah, or Song sparrows. Photographs by S. A. Perkins.

METHODS

Morphology and behavior.—We captured the sparrow on 25 July 1999 and attached a USFWS metal tag on the left leg and two white plastic color bands on the right leg. We measured the exposed culmen, bill depth at tip of nares, bill length from nape to tip, wing chord, tarsus, tail, and distance between the longest primary and longest secondary feathers (Pyle et al. 1997). We aged, sexed, and checked this individual for fat content and molt, and compared these measurements to morphological measurements in Pyle et al. (1997) and Rising (1996), using the appropriate subspecies and geographic region for these comparisons.

We made >20 h of detailed observations of the hybrid's behaviors and songs during the summers of 1999, 2000, and 2001. On 16 July 1999, we recorded songs of the hybrid, a Song

Sparrow, and a Savannah Sparrow using a cassette recorder with a Sennheiser microphone (Macaulay Library of Natural Sounds catalog number 105896). The song was analyzed using a Kay Elemetrics signal analysis workstation. Audio spectrograms were produced using Canary (ver. 1.2.4) with 128-point frame length and 43-Hz frequency resolution. We then compared these recordings to published songs of Song, Savannah, and Grasshopper sparrows (Elliot et al. 1997, Righter and Keller 1999, Fig. 2).

Genetic analysis.—We collected a 0.05-ml blood sample from the presumed hybrid's brachial vein and stored it in a lysis buffer solution for genetic analysis. We isolated total genomic DNA from the presumed hybrid using standard phenol chloroform extraction protocol (Sambrook et al. 1989). A 1.1-kb fragment of the mitochondrial (mtDNA) control region was amplified using Grasshopper Sparrow-specific mtDNA control region primers (NLB unpubl. data) via the polymerase chain reaction. A total of 206 bp of the fragment was sequenced and was visually aligned against 171 Grasshopper Sparrow sequences (NLB unpubl. data) and to the only Song Sparrow sequence available at GenBank (GenBank accession # AF053882). We then determined the number of base pair substitutions among all haplotypes. Unfortunately, we were unable to compare the hybrid's mtDNA to Savannah Sparrow because there were no GenBank submissions for the Savannah Sparrow control region DNA sequence.

RESULTS AND DISCUSSION

Genetic analysis.—The percent sequence similarity among different Grasshopper Sparrow haplotypes was ≥98% (Bulgin 2000), whereas the Song Sparrow haplotype had a maximum of 78% sequence similarity to the Grasshopper Sparrow haplotypes. The hybrid haplotype was identical to one Grasshopper Sparrow haplotype and had a 77% sequence similarity to the Song Sparrow haplotype. The similarity between the hybrid and the Grasshopper Sparrow haplotypes is well within the range of intraspecific variation observed for Grasshopper Sparrow (Bulgin et al. 2003) while the more limited similarity observed between the hybrid and Song Sparrow is representative of a between-species comparison (Bulgin et al. 2003). The mtDNA sequence provided strong evidence that the mother of this individual was a Grasshopper Sparrow and not a Song Sparrow.

Morphological characteristics.—We determined that the sparrow was an after-hatch-year male in 1999 because it had no brood patch but did have a cloacal protuberance (Pyle et al. 1997). This individual was molting heavily on the head and body. In the field, we observed morphological and plumage features that were characteristic of Grasshopper Sparrow: flat head, dark crown with a buffy white median crown stripe, yellow on edge of the wing at the carpal joint, and golden yellow lores (Vickery 1996). The limited streaking across the breast more closely resembled a Savannah Sparrow than a Song Sparrow, but the influence of hybridizing with unstreaked Grasshopper Sparrows could obfuscate this distinction.

The father of this hybrid could have been a Savannah Sparrow or a Song Sparrow. Three of six morphological measurements (nares depth, wing chord, tail) of the hybrid fell within the range of Savannah Sparrows and two of the remaining three measurements (tarsus, primary extension) were slightly longer on the hybrid than reported for Savannah Sparrows (Table 1). Three measurements (wing chord, primary extension, tarsus) fit within the range of Song Sparrows but depth of nares and tail length were considerably smaller in the hybrid. The morphological measurements make it very unlikely that the father was a Grasshopper Sparrow because all six hybrid measurements were beyond the known range of male Grasshopper Sparrows (Table 1). The hybrid's exposed culmen was considerably longer than any of the three species of sparrows (Table 1).

Behavior.—During 1999 and 2000, we observed the hybrid using various perches to sing a simplified Song Sparrow song. We found no evidence of nesting behavior or interactions with other birds during these two breeding seasons. However, in June 2001, we noted that the bird sang different songs than in previous years, alternating between Song Sparrow songs and Savannah Sparrow songs. During this period the hybrid carried food to a specific patch at least three times, presumably a nest site. The hybrid also carried a fecal

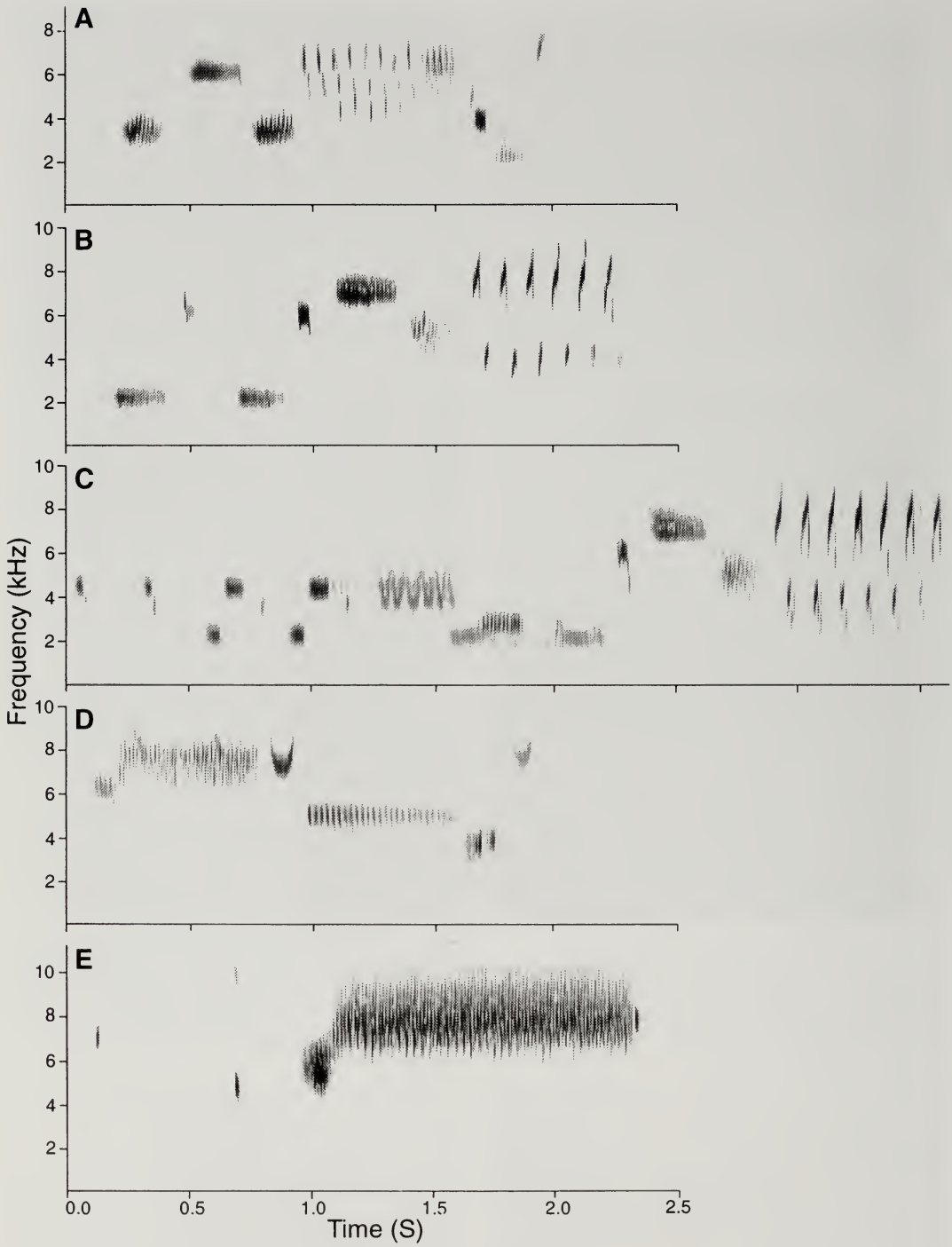

FIG. 2. Audio spectrograms of (A–B) two song types recorded from a presumed Grasshopper × Savannah Sparrow hybrid, and single songs from (C) a Song Sparrow, (D) Savannah Sparrow, and (E) Grasshopper Sparrow. Unlike most Song Sparrows in northeastern North America which have a repertoire of 8–9 songs, the hybrid's repertoire was limited to two song types (A and B). Songs A–D were recorded in Stow, Massachusetts, 16 July 1999, by W. G. Shriver and song E was recorded in Montana (Righter and Keller 1999).

TABLE 1. Body size in male Savannah Sparrows,[a] Song Sparrows,[a] and Grasshopper Sparrows,[a] and the male hybrid sparrow observed in Stow, Massachusetts, July 1999.

Measurement (mm)	Savannah Sparrow	Song Sparrow	Grasshopper Sparrow	Hybrid sparrow
Exposed culmen	9.6–11.9	11.4–13.2	10.5–12.2	14.0
Depth at tip of nares	4.9–6.0	6.3–7.2	5.7–6.3	5.2
Tarsus	18.4–21.6	20.3–23.4	18.3–20.3	22.0
Wing chord	65.0–74.0	61.0–72.0	58.0–65.0	68.0
Distance between longest primary and longest secondary	2.0–7.0	4.0–12.0	—	8.0
Tail	46.0–57.0	61.0–71.0	42.0–50.0	52.0

[a] Measurements from Rising (1996) and Pyle et al. (1997).

sac from this patch and interacted with another sparrow of undetermined gender. When a Savannah Sparrow carried food to the same nest patch, it was repeatedly chased by the hybrid. We saw paired male and female Savannah Sparrows in the vicinity of the nest, and these individuals were aggressive toward the hybrid. By 15 June, the hybrid sang the Savannah Sparrow song only once or twice a day, and we found fledgling Savannah Sparrows near the nest patch. The hybrid remained at this site and was agitated by the presence of other birds, chipping frequently. Later in July 2001, the hybrid repeatedly attempted to copulate with a female Savannah Sparrow and chased other Savannah Sparrows.

We think that the hybrid was more likely genetically related to Savannah Sparrows because of the numerous interactions with Savannah Sparrows and the fact that we never observed it interact with Song Sparrows. There is a previous report of hybridization between Grasshopper and Savannah sparrows (Dickerman 1968), and a case of a female Grasshopper Sparrow "egg-dumping" in a Savannah Sparrow nest (Wiens 1971).

Song.—In 1999 and 2000, the hybrid sang only a simplified Song Sparrow song. In 2001, we observed it singing both Song and Savannah sparrow songs, although it delivered the Song Sparrow song more frequently (>75%, $n > 60$). On at least two occasions, the hybrid alternated between Song Sparrow and Savannah Sparrow songs with no pause between songs. In New England, Song Sparrows (*M. m. melodia*) typically have a repertoire of 8–9 different songs (Peters et al. 2000). Although the hybrid's songs were similar in quality to that of Song Sparrows, it had a repertoire of only two song types (Fig. 2 A–B), which it alternated (A, B, A, B, A, B). Both of the hybrid's song types started with typical Song Sparrow introductory notes, but only song type B ended with the standard Song Sparrow trill (Fig. 2B). The hybrid's song type B was remarkably similar to a Song Sparrow song recorded at the same site (Fig. 2C), providing additional support for the thesis that this bird learned his limited Song Sparrow repertoire from neighboring Song Sparrows. We were unable to record Savannah Sparrow songs from this individual.

Conclusion.—Using four types of information to assess the parentage of this hybrid sparrow, we determined that the mother was almost certainly a Grasshopper Sparrow and that the father was probably a Savannah Sparrow. The mtDNA analysis, indicating the maternal line, showed a close sequence similarity with a Grasshopper Sparrow and we think the morphological analyses, behavior, and song were more consistent with Savannah Sparrow than Song Sparrow for the father. In addition, Song Sparrows have been known to hybridize only with White-crowned Sparrows (*Zonotrichia leucophrys*; Dickerman 1961).

The most unexpected aspect of this Grasshopper × Savannah Sparrow hybrid was the fact that this individual usually delivered a simplified Song Sparrow song. Because song normally is inherited from the paternal line or learned from neighboring males in the nestling stage (Slater 1989), especially from species with high population densities (Jung et al. 1994), the hybrid probably learned these songs from neighboring Song Sparrows whose ranges overlapped with Savannah Sparrows. Although the structure of song was similar to

that of Song Sparrows, the limited song repertoire (two song types) was consistent with that of Grasshopper Sparrows. Hybrid sparrows have been reported to sing a mixture of both parental songs, incorporating elements from each parent, e.g., White-throated Sparrow (*Zonotrichia albicollis*) × Dark-eyed Junco (*Junco hyemalis*; Jung et al. 1994) and Clay-colored Sparrow (*Spizella pallida*) × Field Sparrow (*Spizella pusiila*; Hoag 1999), but we are unaware of a previous case where a hybrid Emberizid sang a song that was not inherited from the father or other conspecifics.

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BREEDING, FORAGING, AND VOCAL BEHAVIOR OF THE WHITE-THROATED JACAMAR (*BRACHYGALBA ALBOGULARIS*)

JOSEPH A. TOBIAS[1,3] AND NATHALIE SEDDON[2]

ABSTRACT.—We studied White-throated Jacamars (*Brachygalba albogularis*) at Manu National Park, Peru, finding a mean population density of 0.8 groups per km of suitable streamside habitat, and taking the first recordings of its song. Observations at nests provided the first evidence of cooperative breeding in the genus *Brachygalba*, as well as information on foraging tactics, prey selection, and provisioning behavior. *Received 27 June 2002, accepted 18 December 2002.*

The Jacamar family (Galbulidae) includes 18 species, all of which are cavity-nesting aerial insectivores confined to the Neotropics (Tobias 2002). Within this family, the genus *Brachygalba* contains four closely related allopatric species, which together form a superspecies (Haffer 1974): the Dusky-backed Jacamar (*Brachygalba salmoni*), Pale-headed Jacamar (*B. goeringi*), Brown Jacamar (*B. lugubris*), and White-throated Jacamar (*B. albogularis*; Fig. 1). A description of breeding behavior has been published for the Pale-headed Jacamar in Venezuela (Skutch 1968), but no such information is available for its congeners, and very little is known about their diet, foraging behavior, and vocalizations (Tobias 2002). To help fill these gaps in knowledge we studied one of the most poorly known members of the family, the White-throated Jacamar, a species restricted to the forests of southeastern Peru, northeastern Bolivia, and western Brazil.

We gathered data over two months (August–September 2001) at Cocha Cashu Biological Station (71° 19′ W, 11° 51′ S), Manu National Park, Peru, a site within pristine lowland, tropical moist forest (see Terborgh 1983 for habitat description). White-throated Jacamars were associated with successional habitat (*Gynerium* cane and bamboo with an open canopy of *Cecropia* trees) in the immediate vicinity of shallow whitewater streams about 5 m wide; indeed, the species has never been observed away from whitewater streams during the many years of fieldwork at the site (J. W. Terborgh pers. comm.). It also seems to be restricted to similar secondary growth at the edge of *várzea* forest and along whitewater streams or broader whitewater rivers in northern Bolivia (Parker and Remsen 1987), and western Brazil (Whittaker and Oren 1999). Its habitat requirements apparently are rather specialized.

We recorded two types of vocalizations during our field work, both of which, being distinctive, constituted the best means of locating the species. The call was a single (though disyllabic) upwardly inflected note (Fig. 2a), corresponding to the "plaintive, upslurred 'psueeet'" mentioned by Parker and Remsen (1987:98) and presented by Schulenberg et al. (2000). It was quite similar to, but slightly huskier and more disyllabic than, the call of the Swallow Tanager *Tersina viridis*, a species that was nesting alongside the jacamars in earthen banks along the creeks. Individual jacamars gave this call fairly frequently throughout the day (generally 1–2 times every few min), but the rate of calling increased markedly when they perched outside nest holes (mean = 10 calls/min ± 12.8 SD, range = 0.7–55.0; data from a 6.5-h observation period on 27 August). Even when several adults sat together on the same perch near the entrance to their nest, calling simultaneously, they were relatively subdued and undemonstrative. They never bobbed the head or raised the crown feathers in the manner of *Galbalcyrhynchus* jacamars, but sometimes flicked the tail and rotated the body from side to side when excited.

On about five separate occasions, while perched high above the ground, at least one of the jacamars gave a more complex (and

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FIG. 1. Three adult White-throated Jacamars waiting to deliver food items to nestlings at Cocha Cashu, Manu National Park, Peru, 27 August 2001. Photograph by Joseph A. Tobias.

previously undescribed) song. This was quite low in volume and weak in tone, beginning with a brief rising twitter, which abruptly decelerated and developed into a descending series of more evenly pitched, emphatic, plaintive notes (Fig. 2b). This general format is similar to the songs, or parts of songs, of other jacamar species in the genera *Brachygalba* and *Galbula* (although members of the latter genus are larger with stronger and richer voices). All White-throated Jacamars seemed rather unresponsive to tape playback, sometimes answering calls or songs but rarely, if ever, approaching.

By repeatedly walking along one white-water stream listening for vocalizations and scanning high *Cecropia* branches, we found that eight groups (mean size = 4.6 individuals, range = 3–6) occupied stable territories along a 6.5-km stretch of suitable habitat (measured along the stream itself). While this roughly equates to one breeding group per 0.8 km, the pronounced meander of streams

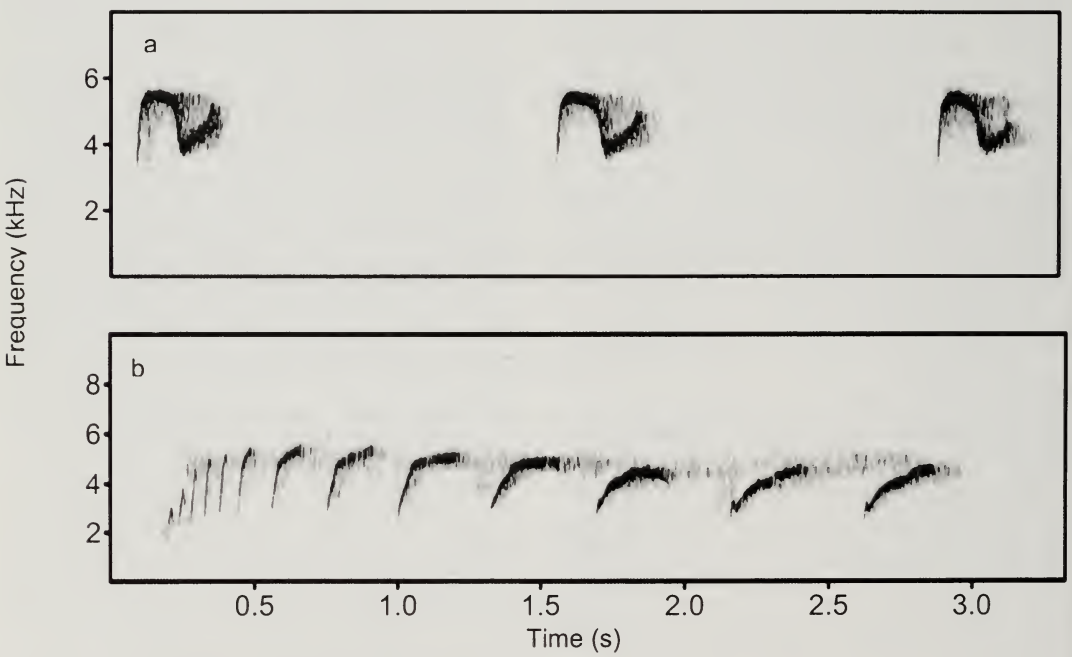

FIG. 2. Spectrograms of (a) the call and (b) song of the White-throated Jacamar, recorded by Joseph A. Tobias at Cocha Cashu, Manu National Park, Peru in August 2001. Using the PC sound analysis software Avisoft SASLabPro, taped recordings were digitized with a 16-bit acquisition card at sampling rates of 16,000 Hz and 22,050 Hz respectively. Calls were filtered to prevent aliasing (low-pass filter, fc = 6,000 Hz) and to remove background noise (high-pass filter, fl = 1,000 Hz). Spectrograms were generated using the following settings: FFT = 512, band width = 235 Hz, frequency resolution = 31 Hz, frame = 50%, window = FlatTop, overlap = 88%.

TABLE 1. Foraging behavior of White-throated Jacamars at Cocha Cashu, Manu National Park, Peru. Data are pooled from 14 timed, focal watches of four individuals on 27 August 2001. A flight of more than 5 m without attempting to capture prey was deemed a switch in foraging area.

Aspect of foraging behavior	Mean ± SD (range)
Perch height (m)	14 ± 4 (5–25)
Sallies (number/h)	40 ± 20 (15–73)
Time interval between sallies (min)	1.4 ± 1.1 (0.2–3.2)
Proportion of sallies successful	0.2 ± 0.2 (0–0.5)
Sally distance (m)	9 ± 6 (1–40)
Time spent in foraging area (min)	2.6 ± 1.2 (0.3–7.8)
Distance between foraging areas (m)	12 ± 7 (5–25)

meant that the direct distance between groups was shorter.

We located four active nests, all in burrows excavated in 1- to 3-m high vertical banks, 2–8 m from the stream, and all partially hidden behind overhanging vegetation such as fallen bamboo. The timing of these breeding attempts (in the middle of the dry season) coincided with peak breeding activity in most other bird species in the humid forests of southeastern Peru (Terborgh et al. 1990). Insect abundance probably is highest at this season. Nest design and placement appeared similar to that described for the Pale-headed Jacamar (Skutch 1968), although that species is not tied to watercourses. The aperture of cavity entrances was small (about 7 cm in diameter); we did not determine the interior dimensions or contents of nests so as to avoid disturbance.

On 27 August we made observations at one nest from 09:00–15:30 (GMT −04:00–02:30). All four adults in the group were feeding an unknown number of young; the adults regularly perched in a row with food items held in the bill (Fig. 1), and entered the nest hole sequentially. A minimum of four adults was feeding young at all four nests observed. This clearly demonstrates cooperative breeding (or at least cooperative provisioning) in this species, the first published evidence of such behavior in *Brachygalba*. Previous evidence for cooperative mating strategies for all galbulid genera has been anecdotal (for the gregarious *Galbalcyrhynchus* and *Jacamaralcyon*), or anomalous (for *Galbula*; Sick 1993, Tobias 2002, E. O. Willis pers. comm.). Nonetheless, the fact that all *Brachygalba* species often are seen in small groups suggests that cooperative breeding will be found to be widespread in the genus.

Adults remained within 80 m of the nest during our observations; they visited the nest 15–20 times/h (mean = 16.2 times/h ± 3.4 SD) with intervals of 3 s to 34 min between visits (mean = 3.9 min ± 0.6 SD). Before entering the nest cavity, they perched on an open branch about 2 m from the nest entrance for 10–312 s (mean = 64 s ± 66 SD), and after entering they remained inside the cavity for 1–48 s (mean = 10.7 s ± 14 SD).

All 92 identified food items brought to the nest hole were insects with a body length of 5–40 mm (mean = 18 mm ± 6 SD, estimated to the nearest 5 mm using the 4.5-cm bill for scale). Of these, 47.8% were hymenopterans, 40.2% were lepidopterans, 11% were small odonates, and there was also a single cicada. Most (15.2%) of the positively identified lepidopterans were skippers (Hesperiidae), and many unidentified prey items probably were from this group; the remainder included several species of brush-footed butterflies (Nymphalidae) and whites and sulphurs (Pieridae). The predominance of skippers in the diet matches Skutch's (1968) observations of the Pale-headed Jacamar.

All four adults collected food by sallying from open perches in 25-m tall creekside *Cecropia* trees, a habit noted previously in western Brazil (Whittaker and Oren 1999). We gathered data on the technique and success of their aerial sallies during 14 foraging bouts of 3–16 min (mean = 8.2 min ± 4.5 SD; Table 1). They performed a mean of 40 sallies/h, a rate comparable to that of the Green-tailed Jacamar *Galbula galbula* (Tobias 2002). This foraging rate presumably was higher than the

basal rate given the demands of chick provisioning; food items were fed to the young after 21% of the successful sallies. Although the observation period spanned the hottest part of the day when many rainforest species are inactive, flying insects were most easily captured at this time and the jacamars therefore foraged busily.

Foraging behavior and prey selection in jacamars is dependent upon the flight periods of insects and the age of nestlings (Tobias 2002). In this instance, nestlings probably were >10 ten days old given the high provisioning rate, the large size of some food items offered, and the fact that food was sometimes provisioned just inside the burrow entrance rather than in the terminal nest cavity. No birds could be found in the vicinity of the nest four days later, and the chicks were presumed to have fledged or been predated.

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SONG STRUCTURE MAY DIFFER BETWEEN MALE AND FEMALE LEAST FLYCATCHERS

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ABSTRACT.—Female song rarely has been examined in suboscines. This paper describes the context and structure of female Least Flycatcher (*Empidonax minimus*) songs. During two years, we observed 4 of 19 females singing, and although singing occurred infrequently, it occurred predominantly at the nest during incubation and brooding. Analysis of five songs from one female showed that the mean of this female's songs fell below the distribution of male songs for the internote interval, the minimum and maximum frequency, the frequency range, and the frequency at maximum amplitude of the first note of the two-note song. These results differ from other studies showing no sex differences in song structure of tyrannid flycatchers, suggesting further analyses of female song are warranted. *Received 23 September 2002, accepted 01 May 2003.*

Female song is known to occur in only a small number of suboscine species, most of which are duetting species found in the tropics (Farabaugh 1982). Cases of female song in migratory suboscines are rare, although there are a few laboratory (Kroodsma 1984, 1985), and field (Mumford 1962, Smith 1969, Seutin 1987) studies. In oscines, female song usually differs from male song (Hoelzel 1985, Arcese et al. 1988, Baptista et al. 1993), suggesting that female song may have a different purpose (Langmore 2000). Sex differences in suboscine song structure rarely have been examined, although testosterone implant studies on captive birds showed no structural differences between male and female song (Kroodsma 1984, 1985). Field observers have drawn similar conclusions, although there are no structural analyses owing to the challenges of recording singing females (Seutin 1987).

Here we examine the occurrence and structure of female song in the Least Flycatcher (*Empidonax minimus*) under natural conditions. The Least Flycatcher is a sexually monomorphic, migratory suboscine with a simple two-note song ("che-bec") used by males in territory advertisement, and which can easily be distinguished from calls due to the intensity and frequency of its use (Briskie 1994). Instances of female song have been documented previously in this species (MacQueen 1950, Mumford 1962, Rappole and Warner 1980), although two of these studies used unmarked birds (MacQueen 1950, Mumford 1962) and none quantified song structure. We observed females singing in eastern Ontario and obtained high quality recordings from one subject. Below we describe the contexts in which females sing and compare the structure of the recorded female's song with a sample of recorded males from the same population.

METHODS

We conducted this study near the Queen's Univ. Biology Station south of Chaffey's Locks, Ontario (44° 34′ N, 76° 19′ W) between May and July during the 2000 and 2001 breeding seasons. A total of 19 paired females was observed (9 during 2000, 10 during 2001). Observations of all females and males began as soon as they arrived on the study site and lasted until the end of the breeding season. Each female was visited and observed daily between sunrise and 14:00 EST for instances of female song.

We recorded all songs during calm and clear conditions using a Marantz portable cassette recorder (Model PMD 222) attached to an Audio-Technica directional microphone (Model AT 815a) through a Saul Mineroff pre-amplifier (Model BA3). We digitized songs using Avisoft SASLab Pro (Specht 1995) at a 22,046-Hz sampling rate and analyzed song structure using a Hamming window and the automatic measurement function

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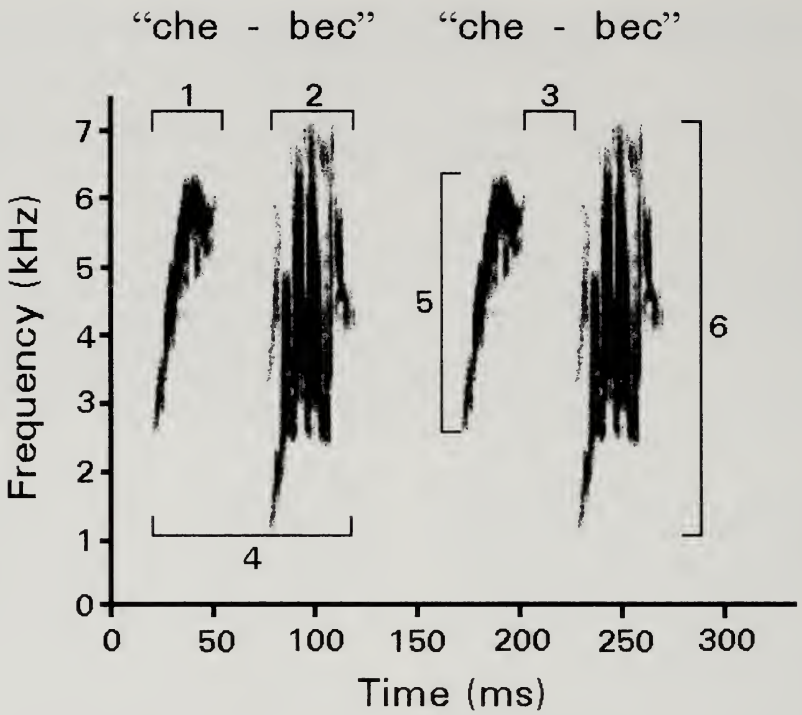

FIG. 1. Structural variables of Least Flycatcher songs: (1) duration of first note, (2) duration of the second note, (3) internote interval, (4) total song duration, (5) frequency range of the first note, and (6) frequency range of the second note; see methods for descriptions of six additional variables. Data are from birds breeding in eastern Ontario, Canada, during 2000 and 2001. Recordings were made by M. M. Kasumovic.

in Avisoft. The parameters during the analysis remained constant and were set up to recognize a threshold of −6 dB for element separation and −10 dB for the calculation of spectrum based parameters. We measured a total of 12 variables. Four of the variable were temporal: the duration of the (1) first and (2) second note, the (3) internote interval, and the (4) length of the total song. Seven of the variables were based on frequency: the frequency range of the (5) first and (6) second note, the minimum (7–8) and maximum (9–10) frequency of each note, and the frequency at maximum amplitude of each note (11–12; Fig. 1). Frequency at maximum amplitude was calculated using Cool Edit 2000 (Johnston 2000).

We captured all recorded individuals using a mist net and banded them with an aluminum Canadian Wildlife Service band and a color band for easier identification. We also collected approximately 30 μL of blood. Females were sexed morphologically in the field (Pyle et al. 1987) and sexing was confirmed later in the lab using a molecular sexing protocol (Griffiths et al. 1998).

RESULTS

Four of 19 females that we monitored during the breeding season were observed singing (two during 2000 and two during 2001). We heard all instances of female song before 10:00 EST during incubation and brooding periods. One female captured during the incubation period sang while held in a bird bag. We observed only one of the four females singing more than one song; all recordings were made from this female. This female was the primary female in a polygynous mating. We heard a total of 13 songs from this female during 4 h of observation on three different days. The female sang eight of these songs while incubating eggs; including two given just before she left the nest. We heard the remaining five songs as the female returned from foraging, after which the nestlings began making begging calls.

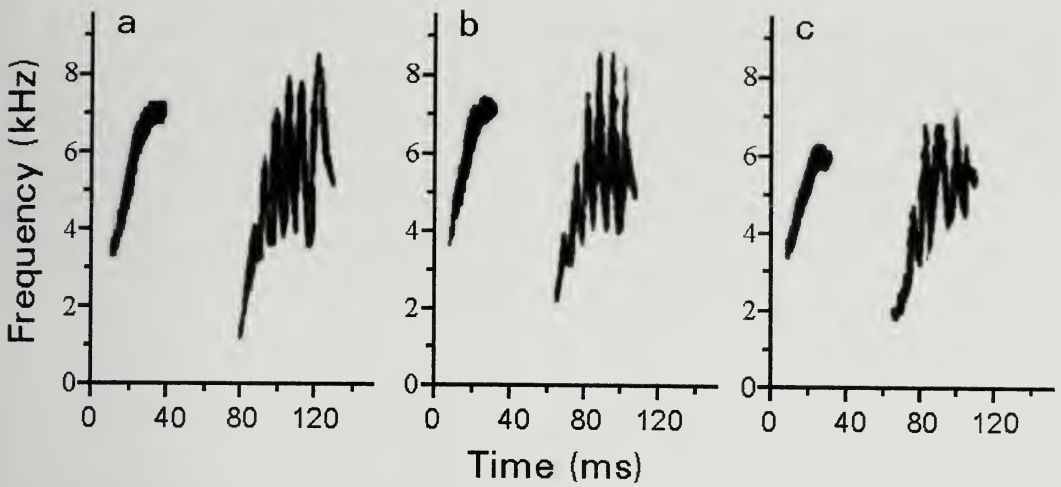

FIG. 2. Sound spectrograms of the songs of Least Flycatchers breeding in eastern Ontario, Canada, during 2000 and 2001; (a–b) two males, (c) one female. Compared to that of males, the first note of the female's song had a lower minimum frequency, lower maximum frequency, lower frequency at maximum amplitude, and a narrower frequency range, and the internote interval was shorter. No differences were seen in the second note. Recordings were made by M. M. Kasumovic.

Because we were able to record songs from only a single female, we did not compare sex differences in song structure with statistical tests of significance. Instead, we calculated a mean for each individual male's songs (based on 5–10 songs from each male, $n = 40$ songs in all), and then examined the means of the female's songs ($n = 5$ songs) with respect to the distribution and the mean of all the males' means. The means of the female's songs fell within the distribution of male means for all except the following five variables, where the mean of the female's songs was below the distribution of the males' means. The first note of the female's song had a lower minimum frequency (female: 4,362 Hz ± 226 SE; males: 5,145 Hz ± 128 SE, range = 4,722–5,576 Hz), a lower maximum frequency (female: 6,006 Hz ± 62 SE; males: 7,064 Hz ± 51 SE, range = 6,876–7,159 Hz), a lower frequency at maximum amplitude (female: 5,655 Hz ± 156 SE; males: 6,637 ± 67, range = 6,355–6,817 Hz), a narrower frequency range (female: 1,644 Hz ± 190 SE; males: 2,462 Hz ± 468 SE, range = 1,814–2,154 Hz), and a shorter internote interval (female: 0.0568 s ± 0.0012 SE; males: 0.0674 s ± 0.0032 SE, range = 0.0602–0.0822 s). Fig. 2 shows the sound spectrogram of a female song (Fig. 2c) compared to two typical male songs from two different males (Fig. 2a, b).

DISCUSSION

Male Least Flycatchers sing at high rates throughout the breeding season (MacQueen 1950). Although females are highly vocal using "whit" and "weep" calls during the breeding season (Briskie 1994), female song is very rare. Our results confirm previous studies stating that female Least Flycatchers sing male-like songs, as seen in other *Empidonax* species (Seutin 1987). A previous study noted that females sang during the nest selection period (Mumford 1962), whereas we observed females singing only during incubation and brooding periods. While it is possible that we missed hearing some female song during the nest selection period, we think this is unlikely as we followed marked females extensively during nest building in order to locate nests.

The results of our structural analysis should be treated with caution since we were able to analyze songs from only a single female. Larger sample sizes are necessary to determine whether male and female songs truly differ in structure. Although females sing male-like songs, our study suggests there may be

sex differences in song structure, with the first note of a female's songs having a lower minimum and maximum frequency, frequency at maximum amplitude, and shorter internote interval than male songs. This finding contrasts with previous studies examining song in a total of five testosterone-implanted female tyrannids where no differences were found (Kroodsma 1984, 1985). It is possible that under natural conditions, female song may serve a different signaling purpose than the aggressive and sexual functions of male song.

A recent study has shown that female Willow Flycatchers (*Empidonax traillii*) aggressively defended territories on the wintering grounds using song (Koronkiewicz 2002). Furthermore, breeding female Willow Flycatchers responded aggressively to intruders (Seutin 1987) and sang from the nest during aggressive interactions (Sogge et al. 1997). We observed similar situations in Least Flycatchers where females also are known to participate in territory defence (MacQueen 1950). The female that we recorded sang most often when her mate was silent and away from the nest. The presence of a secondary female on this male's territory might have increased female aggression as observed in female Yellow Warblers (*Dendroica petechia*; Hobson and Sealy 1990). Finally, one female also sang while being held in a bird bag. Hence, our observations coupled with those on Willow Flycatchers suggest that female *Empidonax* flycatchers may use songs during aggressive interactions, or as a warning in situations of distress. Further studies are necessary to determine whether female song is associated with increased aggression in the absence of the resident male.

Experimental work investigating the song of females in this species may prove interesting, since songs in suboscines are innate rather than learned (Kroodsma 1984). Other species of migratory tyrannids also have been documented to sing (Smith 1969; Kroodsma 1984, 1985; Seutin 1987; Sogge et al. 1997), which suggests that female song in this taxon may be common. More observations of marked birds of known sex are needed to determine the prevalence of female song in other suboscines, and to elucidate its functions.

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A FIELD STUDY OF ORNAMENTS, BODY SIZE, AND MATING BEHAVIOR OF THE GAMBEL'S QUAIL

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ABSTRACT.—Male Gambel's Quail (*Callipepla gambelii*) have strikingly ornate plumage. Yet, captive experiments indicate that removing multiple ornaments does not necessarily alter patterns of female mate choice or male-male competition. To test these unexpected results, I observed a wild population of banded quail for three seasons to determine ornamental and body size traits associated with pairing date and winners of male contests. I also documented mating behaviors (e.g., pairing date, mate fidelity, brood size). Consistent with captive studies, male mass, rather than ornate plumage, was the primary feature related to winners of male contests and early pairing. Heavier males paired earlier, regardless of age, but did not exhibit significantly larger ornaments. Adults of both sexes were heavier and paired earlier than yearlings. Early pairing also correlated positively with brood size, suggesting that heavy, early nesting birds experienced greater fitness. Mating behaviors were flexible across seasons. Social monogamy decreased from 83% in 1996 to 30% in 1998, while polygamy (sequential, long term pairings) increased, particularly among yearlings and adult males. Adult females were equally likely to exhibit social monogamy or polygamy each season. They also exhibited the highest frequency of early pairing and the greatest keel scores (a general measure of condition), suggesting their capacity for breeding was high. At least two adult females abandoned their first mate after hatching and re-paired, in an apparent attempt to double brood. *Received 31 August 2002, accepted 28 February 2003.*

The Gambel's Quail (*Callipepla gambelii*) is a highly sexually dimorphic game bird of the arid southwestern United States. Males exhibit multiple plumage ornaments, such as a long head plume, light and dark belly patches, and a rusty head patch (Johnsgard 1973). Contrary to prediction, tests of captive Gambel's Quail and other galliform birds indicate that many extravagant feather traits of males do not play a primary role during female choice (Beani and Dessi-Fulgheri 1995, Buchholz 1995, Ligon and Zwartjes 1995, Hagelin and Ligon 2001, but see Calkins and Burley 2003) or male-male competition (Ligon et al. 1990, Buchholz 1997, Hagelin 2001a). Even the removal of multiple ornaments in Gambel's Quail and Red Junglefowl (*Gallus gallus*) did not alter patterns of female preference (Ligon and Zwartjes 1995, Hagelin and Ligon 2001). Instead, body size and testosterone-mediated traits often are favored and may function as reliable signals of male quality or condition (Ligon and Zwartjes 1995; Berglund et al. 1996; Hagelin 2001a, 2001b; Hagelin and Ligon 2001).

The principal goal of this study was to test laboratory findings by studying Gambel's Quail in the field. Wild populations typically are male biased (Brown and Gutiérrez 1980), suggesting that ornaments may signal information to discriminating females or male competitors. I aimed to determine the ornamental and body size traits associated with (1) early pairing, which I found to be positively related to reproductive success, and (2) the winners of male contests. I observed a population of banded, free-ranging Gambel's Quail for three seasons (1996–1998) and recorded when mates paired and the outcome of aggressive interactions between males. I predicted that if male ornaments functioned during sexual selection, ornament size would correlate positively with early pairing or male status (Senar and Camerino 1998, Wolfenbarger 1999).

A second goal of the study was to characterize the mating behavior of Gambel's Quail. Though generally considered socially monogamous (Johnsgard 1973), at least one account suggests that double brooding may occur (Gullion 1956). Recent studies have documented multiple broods in other North American quail, and breeding strategies appear to be more flexible than previously surmised (Curtis et al. 1993, Burger et al. 1995, Delehanty 1995, Guthery and Kuvlesky 1998).

To assess mating behavior, I determined (1) the proportion of socially monogamous versus

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polygamous pairs in the population, (2) the sex and age classes of birds that exhibited different breeding strategies, and (3) how mating strategies changed across years. Climatic parameters, such as temperature and rainfall, are thought to influence the fluctuations of quail populations (e.g., Raitt and Ohmart 1967, 1968; Campbell 1968; Heffelfinger et al. 1999; Guthery et al. 2001; Lusk et al. 2001). However, the underlying breeding patterns of different sex and age classes are not well understood.

STUDY AREA AND METHODS

A field assistant and I monitored quail from January 1996 to August 1998 at Bosque del Apache (BDA) National Wildlife Refuge, San Antonio, New Mexico (34° 49′ N, 106° 53′ W). Quail commonly are seen foraging, sunbathing, and drinking within 10 m of a 3-m × 3-m observation window at the BDA visitor's center throughout the year. The habitat consists of open sandy soil interspersed with dense shrubs (four-winged saltbush, *Artemesia tridentata*). Refuge staff provided quail and other wintering birds with approximately 1 kg of wild bird feed (millet, cracked corn, milo, sunflower seeds) daily between December and February.

Trapping and measurements.—We trapped quail near the visitor's center from December to February using funnel traps baited with seed. Each bird received a unique combination of plastic color leg bands. We determined sex from the presence of ornate plumage and age (yearling or adult) from primary wing coverts (Brown et al. 1998). Measures of body size followed Hagelin and Ligon (2001) and included mass and length of tarsus, flattened wing, tail, and culmen. We also palpated the sternal keel (Gregory and Robins 1998) to obtain a general measure of body condition (fat and muscle). We categorized a bird's keel as: 0 (no fat or muscle; sharp keel), 1 (some fat and muscle; moderately sharp keel), or 2 (high fat and muscle; dull keel). Ornament measurements also followed Hagelin and Ligon (2001). Briefly, we measured the flattened plume length of both sexes. We also calculated the area (in mm^2) of ornaments unique to males (light and dark belly patches, rusty head patch) by multiplying patch width and height. We measured rusty head patch in 1997 and 1998 only. We calculated mean trait sizes for birds that were trapped and measured more than once. All quail handling was conducted under Animal Welfare Assurance #A4023-01 and Univ. of New Mexico Animal Care Protocol #9801-B.

Pairing, brood size and hatching date.—Using binoculars, we monitored quail from the BDA observation window from March through mid-August. Observations usually occurred on alternate weeks during hours of peak activity (dawn until late morning, late afternoon until dusk). An observation period typically spanned two consecutive days and totaled 10–30 h of monitoring. An individual was considered paired when it was seen for ≥2 weeks (≥2 observation periods) in close proximity to the same individual of the opposite sex. The behavior of pairs was discernable from unpaired birds; pairs typically distanced themselves from others, followed each other while foraging, and the male usually chased off all other quail. We used only those birds that exhibited obvious changes in pairing status (e.g., unpaired before but consistently seen with mate after 23 April) in analyses of pairing behavior.

We recorded the number and age of chicks that accompanied banded birds. Chick age was estimated in 1-week increments. Raitt (1961) described plumage-based age estimates for California Quail (*C. californica*), which are virtually identical to Gambel's Quail (Raitt and Ohmart 1967). We estimated each brood's hatching date by subtracting the age of a brood (in weeks) from the date we observed it. To determine the median hatching date of the population more accurately, we also included data for unbanded parents with newly hatched broods (<1 week old). We distinguished between new broods during each observation period by the number of young. We avoided problems of duplicate counting, because observation periods took place every other week. Newly hatched chicks of unbanded birds grew markedly between these periods and were not counted again.

Male contests and mating behavior.—Male aggression was common during each season. We noted the band combination, the pairing status of each (whenever possible), and the outcome of encounters between pairs of banded males. "Winning" males caused their op-

ponents to retreat from the immediate area. "Losing" males either retreated immediately, or fled when an opponent escalated aggression.

We recorded the mating behavior of banded birds during pairing and breeding (March through mid-August). Individuals remaining with the same mate throughout this period were considered socially monogamous. In contrast, a bird seen with a partner for ≤2 weeks (approximately the time required to lay a clutch; Gorsuch 1934, Johnsgard 1973), that next associated with another mate for ≤2 weeks, was considered polygamous. We scored polygamy only when we saw both members of the original pair, as to exclude the possibility of mate mortality. We also noted extrapair behavior for birds that partnered with a new mate for one observation period, but had returned to their original, long term mate by the next period. Finally, we recorded breeding and parenting behaviors, including single parents with broods and multiple parents with communal broods.

Statistical analysis.—I calculated the age and sex ratios of the population annually. Differences in trait size between the sexes and age classes (yearling, adult) were assessed with 2-tailed *t*-tests, whereas differences in trait sizes across years were analyzed with ANOVA. Data were tested for normality prior to any parametric test. I used 2-tailed Fisher's exact tests to assess patterns related to keel scores.

I calculated the median pairing date for the population each season. I tallied the number of adults and yearlings that paired before, versus after, the median date and analyzed patterns with Fisher's exact tests. I used chi-square goodness of fit tests to assess age-assortative mating when both members of a pair were banded. MANOVA determined any significant differences in ornaments or body size relative to pairing date, age class, or across the three years studied. Separate MANOVA analyses were conducted for males and females, and each bird was used only once in each data set. Trait sizes were the dependent variables in each MANOVA analysis, whereas pairing date, age and year were independent, categorical variables. Pairing date compared traits of individuals that paired before versus after the median pairing date, and age compared traits between yearlings and adults.

Stepwise discriminant analysis selected the specific traits that best described each significant categorical variable (pairing date, age, or year) from MANOVA analysis. These traits subsequently were analyzed with ANOVA and 2-tailed *t*-tests to determine how they varied relative to categorical variables. Since the rusty head patch of males was measured only in 1997 and 1998, an additional MANOVA model that included the rusty patch was run for males from these two years only. I also used Pearson correlations to clarify the relationship(s) between male ornaments and body size.

I determined the median hatching date annually and estimated the mean size of broods that hatched relative to the median date. Mean brood size was calculated in two ways: brood size of chicks ≤1 week old, and brood size pooled across all other chick ages. I used brood size of newly hatched chicks to estimate clutch size and hatching success, whereas data pooled across ages was used to estimate mean brood size during chick rearing. I tested the relationship between hatch date and brood size with 1-tailed *t*-tests, as late hatching broods typically are smaller (Price et al. 1988). I also compared mean brood size of adult and yearling pairs. Broods of banded birds were not observed frequently enough to determine the total number of young fledged. Therefore, seasonal changes in brood size (see above) were essential to understanding whether early pairing birds also experienced greater reproductive success. This approach was reasonable only if the pairing date of a bird correlated with the hatching date of its brood. That is, birds pairing before the median pairing date also should hatch broods before the median date and *vice versa.* Significance of the association between pairing and hatching was evaluated with a chi-square contingency table.

I used binomial and chi-square tests to determine if winning a contest was related to a male's age class or pairing status (paired versus unpaired). I subtracted ornamental and body size traits of the losing male from the winner to understand how traits related to winning. Winner-minus-loser (W − L) scores were analyzed with Wilcoxon signed rank

TABLE 1. MANOVA and discriminant analysis of Gambel's Quail breeding at Bosque del Apache, New Mexico, indicated that the significant effect of pairing date in males between 1996 and 1998 was best described by differences in mass and not ornaments. The significant effects of year and age were based on differences in ornaments (males) and body size (males and females).

Sex	Effect	*F*	df	*P*	Discriminant analysis[a]	*F*	*P*
Males	Pairing date	2.0	8, 141	0.0506	Mass	9.1	0.0030
	Year	12.4	8, 142	0.0001	Tarsus, tail, dark patch, white patch	14.9	0.0001
	Age	4.6	8, 141	0.0001	Mass, wing, culmen, plume	12.7	0.0001
Females	Pairing date	1.4	6, 101	0.1996	—	—	—
	Year	3.1	6, 102	0.0070	Tarsus, tail	9.0	0.0002
	Age	2.9	6, 101	0.0119	Mass, wing, tail	10.3	0.0001

[a] Variables included mass (g); length (mm) of tarsus, culmen, tail, flattened wing, and flattened head plume; and area (mm^2) of dark and white belly patches.

tests. Each pair of males used in signed rank tests was unique; therefore, W − L scores represented independent data points. When male pairs interacted more than once, the bird that dominated a simple majority of contests was considered the winner, and only one W − L score was included in the data set. Ornaments might operate differently over the course of the breeding season. For example, early contests that occur during pair formation may differ from late season contests that involve mate or chick guarding. Since the pairing status of males was not always known, I conducted signed rank tests on W − L data sets collected before versus after the median pairing date. Given the large number of male traits used in signed rank tests, the risk of Type I error was high, which could have caused some variables to be significant by chance (Rice 1989). Therefore, I analyzed the entire W − L data set simultaneously in a multiple logistic regression with a stepwise selection procedure. The analysis identified traits that best described winning males.

Finally, I determined the number of birds that were socially monogamous versus polygamous each season. I assessed any significant shifts away from social monogamy over the three year period with chi-square contingency tables and two-tailed Fisher's exact tests. Binomial tests analyzed patterns of monogamy: polygamy within each year, as compared to the 50:50 null expectation. I also used a contingency table and Fisher's exact test to determine whether adult or yearling pairs were more likely to act monogamously or polygamously.

RESULTS

Pairing.—We made 618 hours of behavioral observations over three seasons and recorded pairing status for 313 of 450 banded adults and yearlings. Median pairing dates occurred on 14 April (1996), 11 April (1997) and 4 April (1998). Contrary to predictions of ornament size, MANOVA analysis identified the mass of males as the only trait of either sex that correlated significantly with pairing date (Table 1). Regardless of year or age class, heavier males paired before the median pairing date (mean mass of adults before median: 184.5 g, after: 178.5 g, $t_{66} = 3.04$, $P = 0.003$; yearling males before median: 185.5 g, after: 174.5 g, $t_{89} = 3.89$, $P = 0.0002$). MANOVA also identified other traits of both sexes that varied significantly relative to year and age class (Table 1). These are considered separately, below (see Differences between years, age classes, and sexes). Interaction terms (e.g., year × pairing date) were not significant. Results did not differ when data included rusty head patch. Male mass exhibited a weak positive correlation only with dark patch area ($r^2 = 0.025$, $P = 0.056$, $n = 162$; all other ornaments $r^2 \leq 0.0009$, $P \geq 0.70$). Weak correlations between other body size traits and ornaments also were positive ($0.026 \leq r^2 \leq 0.063$, $108 \leq n \leq 170$, $0.001 \leq P \leq 0.095$).

Adults of both sexes were more likely to pair before the median date (66% of 136 adults versus 43% of 177 yearlings, $\chi^2_1 = 15.9$, $P < 0.0001$). This pattern was more marked in adult females (75% of 57 paired early) than adult males (60% of 79, $\chi^2_1 = 3.7$,

TABLE 2. Gambel's Quail broods hatching before the median hatching date were larger than those hatched later in the season at Bosque del Apache, New Mexico. Two ages categories are given: newly hatched chicks (≤1 week) and broods of all other age classes (2–6 weeks). Significance is one tailed, as brood size was expected to decline for late hatching birds.

Year	Brood type	*n*	Mean brood size ± SE		*t*	*P*
			Early broods	Late broods		
1996	≤1 week	28	11 ± 0.6	6 ± 0.9	2.5	0.020
	All ages	35	10 ± 0.9	5 ± 0.5	3.3	0.002
1997	≤1 week	31	12 ± 0.9	8 ± 1.0	1.8	0.080
	All ages	78	11 ± 0.7	7 ± 0.6	2.8	0.007
1998	≤1 week	11	12 ± 1.2	5 ± 0.9	3.2	0.010
	All ages	29	9 ± 0.9	4 ± 0.4	3.2	0.003

$P = 0.054$). Yearling birds showed no such pattern; exactly 43% of females ($n = 83$) and 43% of males ($n = 94$) paired before the median. Of 35 pairs in which both individuals were banded, 26 were the same age (18 adult pairs, 8 yearling pairs), while 9 were of mixed age ($\chi^2_1 = 8.1$, $P = 0.004$). In only four cases, pairs from a previous season mated again the following year; these birds always paired before the median pairing date. No birds paired with the same partner during all three years. Mortality probably inhibited pair bonds >2 years, as we noted it only three times.

Since age was related to pairing and some ornaments correlated with male size, I used multivariate ANCOVA to determine if early pairing males had ornaments that were larger than expected for their body size. For each age class, I regressed male ornaments against two predictor variables: (1) PRIN1 scores from a principle components analysis that described variation in male body size (mass, tarsus, wing, tail), and (2) pairing date, which denoted whether a male had paired before or after the median pairing date. Body size (PRIN1) correlated with significant differences in ornament size, but pairing date did not (adults: PRIN1: $F_{4,33} = 5.08$, $P = 0.003$, pairing date: $P = 0.70$; yearlings: PRIN1: $F_{4,61} = 3.45$, $P = 0.013$, pairing date: $P = 0.30$). Therefore, males pairing before versus after the median date did not differ significantly in ornament size, once body size had been taken into account.

Brood size and hatching.—We recorded the pairing date and estimated the hatching date for 100 birds with broods. Pairing date correlated positively with hatching date in 83 cases ($\chi^2_1 = 43.6$, $P < 0.0001$). Namely, birds pairing before the median pairing date also produced offspring before the median hatching date and *vice versa*. The pattern did not differ significantly between the sexes ($P \geq 0.50$). Median hatching dates fell between 6 June (1996) and 11 June (1998). Broods that hatched before the median date were almost twice as large as those hatched later (Table 2). Adults and yearlings produced similar-sized broods (mean size pooled across all ages of chicks: adults: $n = 53$, mean = 8.0 chicks ± 0.7 SE; yearling: $n = 42$, 8.0 chicks ± 0.8 SE). We observed 15 single parents (nine male, six female) tending broods. In five instances (three female, two male), foster parenting apparently occurred, in which a single parent and brood associated with a new mate, and remained together during and following chick rearing. Broods also merged. In five cases, 3–5 parents tended excessively large numbers of chicks (mean brood size = 30 chicks ± 7 SE).

Male contests.—We observed 110 aggressive encounters between different pairs of banded males. Mated males won contests against unpaired opponents 29:4 (binomial test, $P < 0.0001$), and adults tended to dominate yearlings 36:22 ($\chi^2_1 = 3.6$, $P = 0.056$). When both males were paired but differed in age, either male was likely to win (18:17).

Winning males were larger than losers with respect to mass (mean W − L score: 4.7 g, $w = 1210$, $n = 103$, $P < 0.0001$). No ornaments correlated with winning ($P \geq 0.50$). I obtained a similar pattern relative to the median pairing date (mean W − L score pre-median: 3.8 g, post-median: 5.1 g; $200 \leq w \leq 556$, $0.008 \leq P \leq 0.020$, $33 \leq n \leq 70$; all ornaments $P \geq 0.30$). Stepwise logistic analysis also selected

mass as the primary variable that accounted for the differences between winners and losers ($-2\log L\chi^2_1$ estimate: 12.8, $P < 0.001$).

Mating behavior.—Of 164 birds followed during breeding, 56% were socially monogamous and 44% were polygamous. Social monogamy in the population declined from 83% in 1996 to 30% in 1998, while polygamy increased ($\chi^2_2 = 31.5$, $P < 0.0001$). Significant shifts away from monogamy occurred in both sexes of yearling birds (males: Fisher's exact $P = 0.004$; females: $P = 0.001$; Fig. 1A, B) and adult males ($P = 0.001$; Fig. 1C). Adult females, however, were equally likely to exhibit social monogamy or polygamy each year ($P = 0.90$; Fig. 1D). Adult males exhibited a higher frequency of social monogamy (mean = 67%; Fig. 1C), compared to yearlings (51%; Fisher's exact $P = 0.028$; Fig. 1A, B). Pairs of adults tended to be more monogamous (50% of 26) than paired yearlings (27% of 37; Fisher's exact $P = 0.062$). The polygamous behavior of adult females (Fig. 1D) tended to differ from all other members of the population combined (Fig. 1A–C; Fisher's exact $P = 0.061$). We excluded 23 birds from analyses that appeared to act polygamously, but for which we could not exclude the possibility of mate mortality.

A majority of socially monogamous birds (59%) exhibited at least one short (<2-week) extrapair bond. All returned to and tended any chicks with their original mate. Most polygamous birds (78%) exhibited long term, sequential pairings. For example, a banded pair, male blue-left (BL) and female yellow-right (YR), remained together between 4 April and 13 May. By 31 May, BL associated with another female and remained with this mate through the end of the breeding season. YR also paired with another male. Polygamous birds typically switched mates one to two times during a season (e.g., in May and again in June or July). Two adult females in 1996 abandoned their mates and 5- to 6-week-old broods and re-paired with new partners. Three pairs that separated early in the season (May), and had acquired new mates, reunited again later in July. Two reunited pairs were tending a brood.

Differences between years, age classes, and sexes.—Both year and age were significant effects in the MANOVA model (Table 1). Discriminant analysis indicated that the size of ornamental patches of males varied significantly among years, but not between age classes (Tables 1, 3). Two body size traits of both sexes (tarsus, tail length) also varied among years (Table 1). Both decreased slightly over the study period (mean tarsus of both sexes, 1996: 32.1 mm, 1997: 31.2 mm, 1998: 30.8 mm; $F_{2,448} = 38.1$, $P < 0.0001$; mean tail, 1996: 100.2 mm, 1997: 99.0 mm, 1998: 97.5 mm; $F_{2,444} = 5.0$, $P = 0.001$).

Discriminant analysis distinguished between age classes of both sexes on the basis of body size (mass, wing, tail, culmen; Table 1). Adults were larger than yearling birds (mean mass, adult male: 182.4 g, yearling: 176.7 g, $t_{244} = 3.18$, $P = 0.002$; adult female: 179.8 g, yearling: 172.4 g, $t_{201} = 2.97$, $P = 0.003$; wing, tail, culmen: $199 \leq n \leq 249$, $2.3 \leq t \leq 3.4$, $0.0008 \leq P \leq 0.007$). Length of head plumes varied relative to age class in males only (Table 3). Surprisingly, plumes of adult males were slightly, but consistently, shorter than yearling males (Table 3; mean adult: 40.9 mm, yearling: 42.1 mm; $t_{246} = 3.18$, $P = 0.002$).

Males were somewhat larger than females, regardless of age (mean mass, male: 178.8 g, female: 173.0 g, $t_{447} = 3.0$, $P = 0.003$; wing, male: 117.6 mm, female: 115.4 mm, $t_{448} = 8.27$, $P < 0.0001$; tarsus, male: 31.7 mm, female: 30.8 mm, $t_{448} = 7.46$, $P < 0.0001$; tail, male: 101.0 mm, female: 96.1 mm, $t_{444} = 6.87$, $P < 0.0001$; culmen, male: 11.4 mm, female: 11.2 mm, $t_{446} = 2.89$, $P = 0.004$; plume: male: 41.7 mm, female: 31.3 mm, $t_{446} = 46.17$, $P < 0.0001$). We palpated the keel of 163 quail. Ten of 18 adult females obtained the highest score, indicating they had the greatest amount of muscle and fat on their breasts, compared to only 26% of all other birds (Fisher's exact $P = 0.014$).

Population changes.—The 450 Gambel's Quail trapped at BDA exhibited a male-biased sex ratio, due to a scarcity of adult females each year and an over abundance of yearling males in 1998 (Table 4). The age distribution of the population also shifted. In 1996, yearlings were approximately 20% more common than adults, but by 1998, they were 50% more common (Table 4). The resulting 30% increase in the relative abundance of yearling

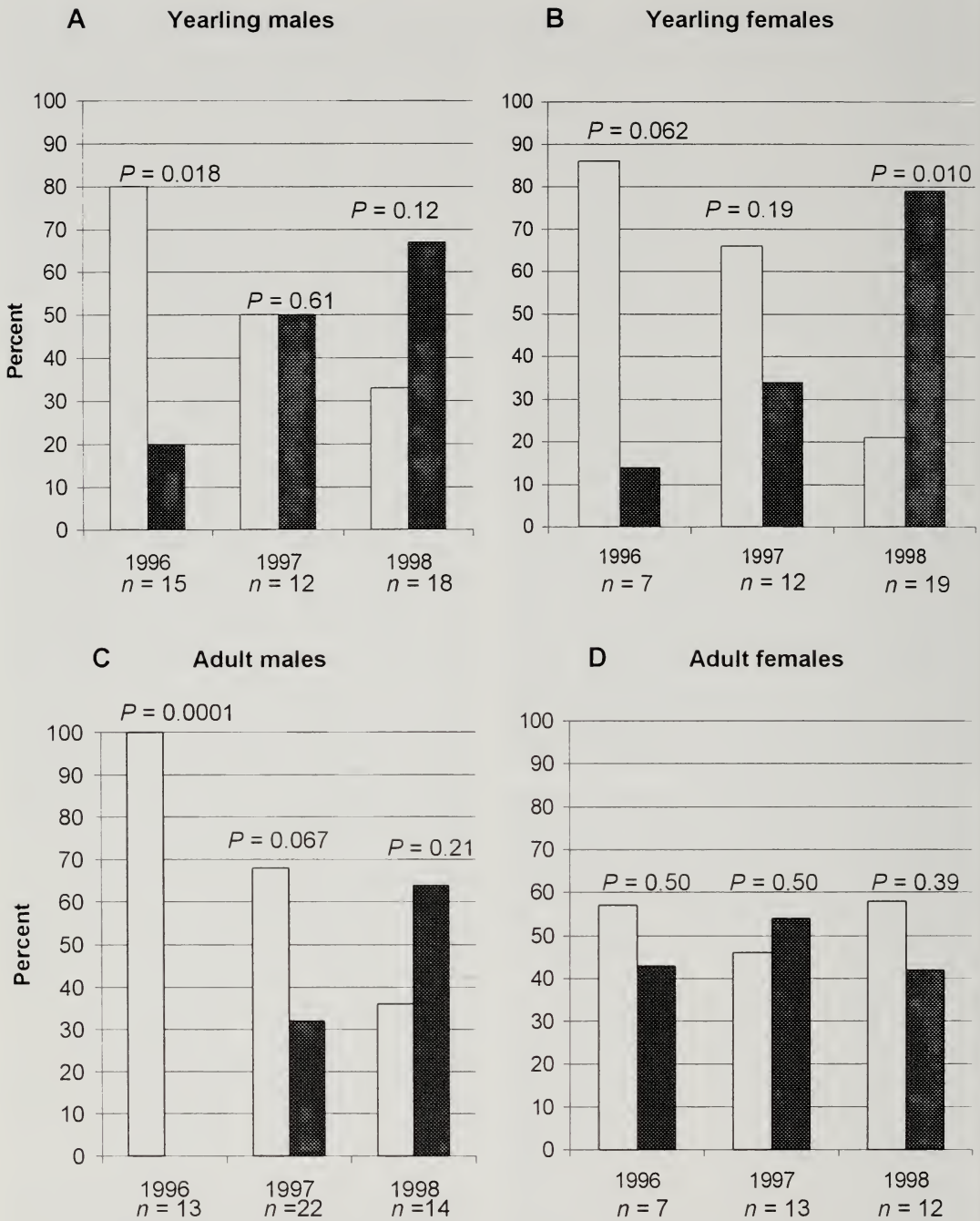

Fig. 1. Significant shifts away from monogamy occurred across years for all groups of Gambel's Quail at Bosque del Apache, New Mexico, except adult females: (A) yearling males, Fisher's exact $P = 0.001$; (B) yearling females, $P = 0.001$; (C) adult males, $P = 0.001$; and (D) adult females, $P = 0.90$. Open bars are monogamous individuals, solid bars are polygamous individuals. Patterns within each year were compared to the null expectation of 50:50 (monogamy : polygamy); the cumulative binomial probability $P(x \geq k)$ for each is given above the bars.

TABLE 3. Ornament sizes of male Gambel's Quail at Bosque del Apache, New Mexico, varied by year and by age class between 1996 and 1998. Contrary to prediction, adult males did not have larger ornaments than yearlings. Significant differences across years or between age classes are indicated in the Trait and Age columns, respectively. Rusty head area was not measured in 1996.

Trait	Age	1996 (n = 66)	1997 (n = 82)	1998 (n = 100)
Dark patch area (mm^2)**	Yearling	1407.4	1111.0	1356.7
	Adult	1431.2	1092.8	1636.8
White patch area (mm^2)**	Yearling	1990.7	1482.9	1738.3
	Adult	1977.9	1478.1	1881.9
Rusty head area (mm^2)*	First-year	—	489.1	514.8
	Adult	—	487.7	527.6
Plume (mm)	Yearling**	42.5	43.0	41.5
	Adult	41.5	41.0	39.5

* $P = 0.05$, ** $P = 0.001$.

birds was significant ($n = 450$, $\chi^2_2 = 8.3$, $P = 0.016$).

DISCUSSION

Ornamental versus body size traits.—Field observations of Gambel's Quail were consistent with the results of captive experiments. Instead of ornaments, male body size, specifically mass (Table 1), was the primary trait that correlated with early pairing and winners of male contests. In captive tests, the body size traits and behavior rates of males were primarily related to female preferences and the winners of male contests, whereas natural variation of single ornaments and experimental removal of multiple ornaments was not (Hagelin 2001a, 2001b; Hagelin and Ligon 2001).

Heavier (and older) males at our field site also were the best competitors. Mass was the primary trait related to winning early season contests and the only trait that varied significantly relative to pairing date (Table 1), indicating that mass (or male size) may influence mate acquisition. In the related California Quail, only those birds that belonged to a male dominance hierarchy were successful in obtaining a mate (Mastrup 1987).

Unlike mass, male ornaments varied significantly among years and between age classes (Tables 1, 3). Flexibility of ornament size suggests that ornaments potentially could serve as indicator traits during some years. Yet, patches were not predictably larger (or smaller) in adults (Table 3), and all ornaments exhibited rather weak correlations with mass and body size traits. Although early pairing males were heavier (Table 1), discriminant and ANCOVA analyses indicated they did not exhibit significantly larger ornaments than other birds in the population. Early pairing, however, resulted in larger broods (Table 3), suggesting that heavier males experienced greater success, regardless of ornament size. Interaction terms of the MANOVA model (e.g., year × pairing date) also were not significant, indicating the relationship between ornaments and pairing date did not change from year to year. The failure to detect any significant pattern of ornaments relative to pairing date (Table 1) did not result from a general lack of statistical

TABLE 4. Yearling and adult Gambel's Quail trapped at Bosque del Apache, New Mexico, exhibited a male-biased sex ratio (% males), a scarcity of adult females, and an increase in the relative abundance of yearlings between 1996 and 1998.

	Males (n)			Females (n)			% Males (%)			Age distribution (%)		
Age	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998
Yearling	35	53	75	35	52	63	50.0	50.4	54.3	59.8	70.0	75.4
Adult	31	29	25	16	16	20	66.0	64.4	55.6	40.2	30.0	24.6
Total	66	82	100	51	68	83	56.4	54.6	54.6	100.0	100.0	100.0

power. Samples were capable of detecting intermediate and large effects of ornament size relative to pairing date, while retaining 80% statistical power (Cohen 1988). Understanding smaller effects of ornaments will require larger samples or perhaps the use of composite indices to enhance the combined effect of multiple ornaments (Calkins and Burley 2003).

In previous captive manipulations (Hagelin 2001a), only one ornate trait, the head plume of Gambel's males, affected the outcome of aggressive contests. Hagelin (2001a) suggested that plume position (erect versus flattened) affected contests, rather than differences in plume length. Field observations confirmed lab findings. Natural variation in plume size did not correlate with winning or early pairing. Adult males, which were larger and usually dominated yearling males, actually had slightly (but significantly) shorter plumes (5% or 1–2 mm; Table 3). Any social benefit of slightly longer plumes appeared to be minimal for yearlings. They were unlikely to win contests or pair early, regardless of plume size.

Several investigations of ornately-feathered species within the order Galliformes have reported similar, and equally counter-intuitive results to those of Gambel's Quail. Specifically, a strong relationship frequently is lacking between the ornate plumage of males and breeding behavior in species such as the Red Junglefowl (*Gallus gallus*; Ligon et al. 1990, Ligon and Zwartjes 1995), Wild Turkey (*Meleagris gallopavo*; Buchholz 1995, 1997), and Grey Partridge (*Perdix perdix*; Beani and Dessi-Fulgheri 1995). Even the simultaneous removal of multiple ornaments did not alter patterns of female preference (Ligon and Zwartjes 1995, Hagelin and Ligon 2001). Rather than a direct involvement of ornaments in sexual selection, many traits appear to have lost their key signaling function and, instead, may be maintained through alternative mechanisms, such as weak selection (Möller and Pomiankowski 1993, Hagelin and Ligon 2001). It is unclear, however, how weak sexual selection must be in order to maintain ornaments. Our data revealed a poor correlation between body size and ornate traits, which may be a sufficient mechanism for ornament maintenance.

If certain plumage ornaments do not reflect male quality, sexual selection may operate on other, more reliable traits (Kodric-Brown and Brown 1984, Möller and Pomiankowski 1993, Hill 1994). Body size generally is thought of as an honest signal, because it is related to an underlying quality that cannot be faked (Maynard Smith and Harper 1988, Guilford and Dawkins 1995, Taylor et al. 2000). Body size of wild quail was clearly linked to age, size, early pairing in both sexes (see also Mastrup 1987), and to male status. Given that Gambel's Quail do not usually live beyond their first breeding season (Sowls 1960), both size and age appear to honestly indicate an individual's overall breeding quality. Experiments using captive quail were consistent with these results; females typically preferred larger males and larger males also won male contests (Hagelin 2001a, Hagelin and Ligon 2001). High keel scores (greater fat and breast muscle) were also associated with age and large size of wild adult females, which may reflect a greater potential for reproduction (Reynolds 1997).

Rather than assessing each ornament separately, Calkins and Burley (2003) considered "composite traits" by combining multiple ornaments of California Quail in analyses of female choice. The exact role, if any, of composite traits in Gambel's Quail is presently unclear. Manipulations that removed both single and multiple ornaments from captive yearling males did not alter mating preferences of females (Hagelin and Ligon 2001). Ligon and Zwartjes (1995) have reported similar results for Red Junglefowl.

Mating behavior.—Gambel's Quail exhibited a flexible breeding strategy which changed markedly from 83% monogamy in 1996 to 70% polygamy in 1998. The resulting 53% increase in polygamy within the population was due to two factors. First, the frequency of polygamy increased in yearling birds and adult males between 1996 and 1998 (Fig. 1A–C). Second, the relative abundance of yearlings increased by 30% over three years (Table 4), and yearling pairs were more likely to exhibit polygamy than adults.

Although the proximate cues underlying individual breeding behavior are unknown, the environmental conditions that influence the irruptive nature of semi-arid quail populations (Forrester et al. 1998, Heffelfinger et al. 1999,

Guthery et al. 2001) appear to provide a mechanism. Extreme heat or lack of precipitation, for example, can influence brood failure (Heffelfinger et al. 1999, Guthery et al. 2001), thereby increasing the frequency of re-pairing. High levels of polygamy at our study site (1998; Fig. 1A–C) coincided with a ten-year low in rainfall at the time of hatching (June), whereas high levels of monogamy (1996; Fig. 1A–C), corresponded to a 25-year high.

Mean mass of both sexes at Bosque del Apache was within the range reported for other wild populations (160–200 g; Brown et al. 1998), suggesting that birds were not abnormally fattened by supplemental winter feed. However, feed could have created a high local nesting density, thereby enhancing re-pairing opportunities relative to other breeding sites. Though absolute measures may differ, the relative changes I observed in brood size (Table 2) and in the breeding behavior of individuals (Fig. 1A–C) occurred independently of winter feed, which remained constant throughout the study.

Adult males, the largest, most dominant birds in the population, exhibited the highest frequency of social monogamy (Fig. 1A–D), indicating monogamous behavior was a preferred breeding strategy. Male California Quail also exhibited an unwillingness to behave polygamously, even during manipulations of sex ratio (see Lott and Mastrup unpubl. data in Calkins et al. 1999). Our data provide several insights into why social monogamy may be favorable. First, pairing date and age-assortative mating indicated that adult males had a good chance of obtaining a quality mate (a large adult female) early on. Heavier adults that paired early had a high likelihood of successful breeding (Table 2), and some adult females attempted second broods. Were a male to abandon its first mate and re-pair, it would be difficult to obtain another mate, particularly an adult female, given their scarcity in the population (Table 4).

Adult females consistently maintained a mean frequency of 46% polygamy, regardless of year (Fig. 1D). This pattern was unlike the more variable breeding behavior of other members of the population (Fig. 1A–C). Adult females also had the highest keel scores and were more likely to pair before the median pairing date than any other birds in the population, indicating they had a high potential for reproduction (Table 2). A male-biased sex ratio (Table 4) and high keel scores may have provided adult females with the opportunity to behave polygamously and obtain additional matings. Accordingly, adult females were the only birds that attempted to double brood. Though male incubation in the Northern Bobwhite (*Colinus virginianus*) contributes to female abandonment and double brooding (Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995), it is unknown in Gambel's Quail. In the California Quail, a related species that occasionally double broods (Francis 1965), male brood patches are rare and may develop only after the death of a mate (Calkins et al. 1999).

Gambel's Quail at Bosque del Apache exhibited both biparental and uniparental care. Birds also showed communal brooding and the potential for foster care. Communal broods in California Quail can provide fitness benefits (Lott and Mastrup 1999). However, both communal brooding and foster care are unstudied in Gambel's Quail.

In conclusion, the traits related to successful breeding in a wild population of Gambel's Quail were consistent with captive studies that assessed the role of both single and multiple plumage ornaments. Early pairing in males was related to mass and age rather than to ornament size. Male mass was also the primary trait associated with winners of male contests. The mating behavior of Gambel's Quail was flexible. Most birds exhibited a shift in breeding strategy from monogamy to polygamy in three years. Adult females, however, exhibited both strategies with equal frequency. Future investigations should aim to understand the mechanisms that cause shifts in breeding behavior and the costs and benefits of different mating strategies. Studies will require detailed data from radio-tagged breeders under known environmental conditions and estimates of brood paternity, in order to compare the annual and lifetime reproductive success of different sex and age classes.

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DISTRIBUTION, ABUNDANCE, AND BREEDING BIOLOGY OF WHITE TERNS ON OAHU, HAWAII

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ABSTRACT.—White Terns (*Gygis alba*) are common in the northwestern Hawaiian Islands, but in the main Hawaiian Islands they are found only on Oahu, where they are listed as threatened by the State of Hawaii. I censused the White Tern population on Oahu from October 2001 to January 2003, and I investigated breeding success and seasonality during monthly visits to four sites. I observed a total of 694 adult White Terns on Oahu, of which approximately 500 (72%) were breeding birds. Active nests were present during all months, but most eggs were laid from January to April (65%), with a peak in egg laying during March (22%). Nest success was 74%, and pairs produced a mean of 0.98 fledglings/year. One pair fledged successive young less than three months apart. The incubation period at one nest was 35 days, and the fledging periods at two nests were 43 and 47 days. The White Tern population on Oahu has increased from a single breeding pair in 1961 to approximately 250 pairs in 2002, a growth rate of 14% per year. White Terns on Oahu exist entirely in urban and suburban areas, and their reproduction is not inhibited by the numerous predators and sources of disturbance. *Received 4 March 2003, accepted 15 August 2003.*

The White Tern (*Gygis alba*) is a common seabird that nests on many islands throughout the tropical and subtropical Pacific, Atlantic, and Indian oceans (Harrison 1983). White Terns are abundant on some of the atolls and rock pinnacles in the northwestern Hawaiian Islands, but in the main Hawaiian Islands they are found only on Oahu (Harrison 1990, Niethammer and Patrick-Castilaw 1998), where a single pair first was observed nesting in 1961 (Ord 1961). The population on Oahu was estimated to be 50–100 pairs in the mid-1980s (Harrison 1990), and a long term study of the breeding biology was conducted in one area of Oahu (Miles 1985, 1986), but there have been no systematic surveys of their distribution or abundance. The White Tern population on Oahu was listed as threatened by the State of Hawaii in 1986 (Hawaii Administrative Rules, Title 13, Part 2, Chapter 124), presumably based on its limited distribution and small population size. I censused the White Tern population on Oahu from October 2001 to January 2003 to provide more recent and accurate information on their distribution and abundance, and I re-examined the breeding biology in several areas of Honolulu.

METHODS

I located White Tern breeding and roosting sites in Honolulu (21° 12′ N, 157° 30′ W) by observing flying birds or by the distinctive clusters of white droppings that accumulated on the ground. I surveyed each location where terns or their droppings were present on at least two different days, and I counted the numbers of breeding and nonbreeding birds. I counted birds as breeding if they were attending an egg or a chick or if they were perched <1 m from a chick that did not appear agitated. Chicks >1 week old appear agitated when approached by an adult other than their parents (Niethammer and Patrick-Castilaw 1998). I counted birds as nonbreeding if they did not appear to be associated with an egg or chick. I counted recently independent young, which could be recognized by their shorter bill with less extensive bluish coloration at the base and the narrower ring of black skin around the eye (Niethammer and Patrick-Castilaw 1998, pers. obs.), as nonbreeding birds.

I assumed that each nest had two adults, and I calculated the number of birds at each location as twice the number of nests plus the number of nonbreeding birds. I then estimated the total population by adding the largest numbers of birds observed at each location. I conducted surveys within 2 h of sunrise because many terns leave nest and roost areas by that time to forage at sea (unpubl. data). This method may underestimate the total population because an unknown number of nonbreeding birds could have been away at sea and missed on each visit. It also is possible that I missed a few smaller breeding and roosting sites.

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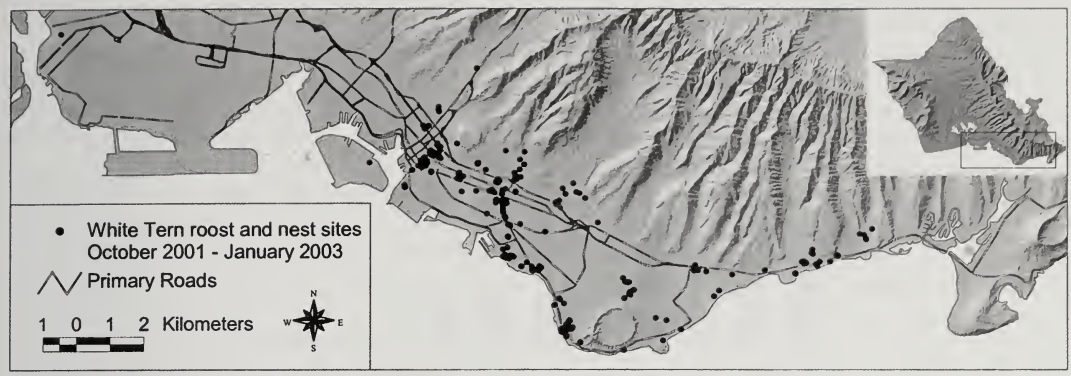

FIG. 1. Distribution of White Tern breeding and roosting sites on Oahu from October 2001 through January 2003. Sites often were loosely aggregated, and all sites were located in urban and suburban areas of Honolulu.

I monitored breeding success by conducting monthly surveys from October 2001 to January 2003 in four areas. Two of these areas contained large concentrations of terns (Kapiolani Park and Kalakaua Avenue), and two areas contained only a few pairs (Beretania Street and Niu Valley). Some pairs in the study areas probably nested more than once per year, based on observations of pairs simultaneously caring for eggs and fledged young and on repeated use of the same nest sites in rapid succession. At Tern Island, French Frigate Shoals, 75% of pairs used the same site for re-laying attempts and in subsequent years (Niethammer and Patrick-Castilaw 1998), and 81% of pairs used the same breeding site two years in a row at Ascension Island (Dorward 1963). At my study areas, none of the birds were marked, so it was not possible to determine with certainty whether some nests were re-laying attempts. The numbers of birds and breeding attempts in months that were surveyed twice (October to January) are presented as means.

RESULTS

I observed a total of 694 adult White Terns and 221 nests on Oahu from October 2001 through January 2003. Based on observations from intensively monitored sites, approximately 72% of the population, or 500 birds, were breeders (see below). All terns were found in urban and suburban areas of Honolulu on the southern shore of Oahu (Fig. 1); no terns were found in other parts of the island. Terns were scattered around many parts of the city, but they often occurred in loose aggregations. In areas where tern density was low, each tree usually contained a single pair, but in more densely populated areas up to four pairs and several nonbreeding birds used a single large tree. Nests occurred as close as 4 m apart.

In the four sites that were monitored monthly, I observed a total of 184 terns and 88 nests. These nests appeared to have been made by 66 pairs, or 1.33 attempts/pair/year by 72% of the population. Sixty-five of the 88 nests were successful (74%), for a mean of 0.98 fledglings/pair/year. There was no significant difference among the four study sites in success of nests (ANOVA: $F_{3,59} = 2.00$, $P = 0.12$). In Niu Valley the incubation period at one nest was 35 days, and the fledging periods at two nests were 43 and 47 days. One pair was observed simultaneously incubating an egg and feeding a recently fledged chick that still had wisps of down. The eggs in those nests were laid in February and May, and the young fledged <3 months apart. In several cases, independent young continued to roost near pairs that began nesting in the same site that just had been used.

Active nests were present during all months, but most eggs were laid from January to April (65%), with a peak in egg laying during March (22%; Fig. 2). Breeding and nonbreeding birds were present all year, but the number of birds was highest during the peak nesting period from February to July, and the fewest birds were present from November to January (Fig. 3).

More than 31 tree species were used for

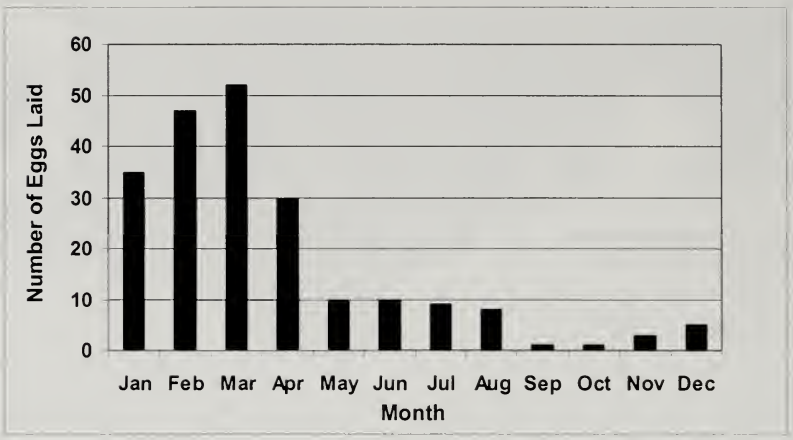

FIG. 2. Seasonality of White Tern breeding on Oahu from October 2001 through January 2003. Most eggs were laid in March, but active nests were present during all months.

nesting and roosting, but banyans (*Ficus* spp., 22%), monkeypod (*Samanea saman*, 13%), mahogany (*Swietenia mahogany*, 13%), and kukui (*Aleurites moluccana*, 10%) were used most often. Banyans and monkeypod are very common in Honolulou, so their frequent use is not surprising, but mahogany and kukui are uncommon and may be preferred by terns. Most trees used by White Terns were among the largest in the area, and White Terns seemed to select larger trees for roosting and nesting.

DISCUSSION

The White Tern population on Oahu, though still relatively small and restricted in range, is increasing and robust. From a single breeding pair in 1961 (Ord 1961), the breeding population increased to approximately 250 pairs in 2002, a growth rate of 14% per year. This rapid population growth has been possible at least partly because of a high reproductive rate. Despite the many sources of disturbance and numerous predators in urban Oahu, reproduction of White Terns in Honolulu reported in this study (74% nest success, 0.98 young/pair/year) and by Miles (1985; 76% nest success) was higher than at Ascension Island (29% nest success; Dorward 1963) or Tern Island (30% nest success, 0.59 young/pair/year; Niethammer and Patrick-Castilaw 1998). Some areas used by White Terns on Oahu, such as Kalakaua Avenue and Waikiki, experience heavy pedestrian and vehicular

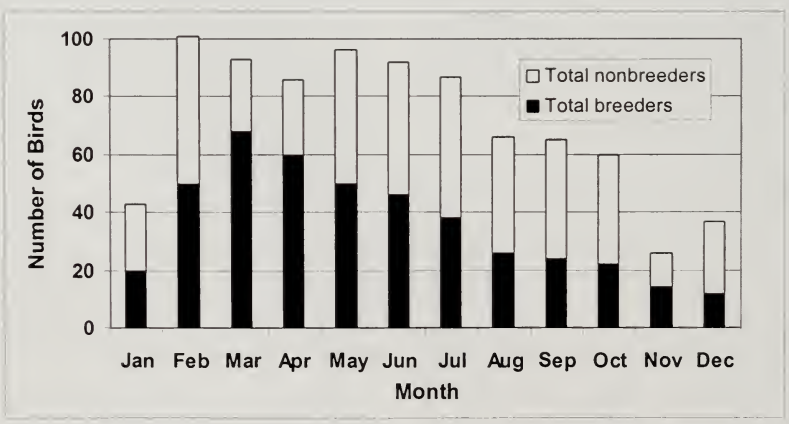

FIG. 3. Seasonal abundance of White Terns at Kapiolani Park and Kalakaua Avenue, Oahu, from October 2001 through January 2003. The peak in numbers of birds coincided with the peak in nesting activity.

traffic virtually 24 h/day, but this does not inhibit reproduction of White Terns, and it is possible that vehicular traffic actually protects tern nests by preventing predators from reaching nest trees. Several times on Kalakaua Avenue I saw dead rats (*Rattus* sp.) and feral cats (*Felis silvestris*) that presumably had been killed by vehicles.

The fledging period on Oahu (45 days) also was shorter than fledging periods reported from Tern Island (53.2 days, Pettit et al. 1984; 48.6 days, Niethammer and Patrick-Castilaw 1998), and Ascension Island (65–70 days; Dorward 1963). Although the rate of development is slower than in some other species, such as Black Noddies (*Anous minutus*; Pettit et al. 1984), White Terns can re-lay rapidly and produce multiple broods per year. Miles (1985) reported White Terns producing broods five months apart and up to three broods per year. During this study pairs raised broods as little as three months apart. The proportion of breeding birds reported in this study (71%) also was higher than that reported from the northwestern Hawaiian Islands (37%; Niethammer and Patrick-Castilaw 1998).

The rapid development, high nest success, high proportion of breeding birds, and consequent rapid growth of the White Tern population on Oahu may be related to food availability near Oahu, the small population size of White Terns on Oahu, and the broad diet of White Terns (Diamond 1982). In the Black Noddy, food abundance is thought to be an important determinant of the number of clutches per year (Gauger 1999). Examination of feeding rates and diet on Oahu might help elucidate the success of this population. The rapid rate of population growth also suggests that survival and site fidelity of juveniles is high, or that there is immigration from other islands, or both.

White Terns currently are found only along the southeastern coast of Oahu, where they breed and roost exclusively in large trees, but on other islands White Terns nest on low vegetation, human structures, and even on the ground (Rauzon and Kenyon 1984, Niethammer and Patrick-Castilaw 1998). On Oahu, White Terns probably are limited to large trees for nesting because they provide relative safety from predators, and the distribution of White Terns on Oahu may be restricted in some areas by lack of large trees for nesting. No White Terns occur west of Hickam Air Force Base or east of Niu Valley, perhaps because these are the last areas in each direction that have groups of large trees. Nests on low vegetation or on the ground would be very unlikely to survive on Oahu due to the abundance of feral cats, mongoose (*Herpestes auropunctatus*), and rats (Smith et al. 2002). When White Terns were studied in Kapiolani Park by Miles (1985), many pairs nested in ironwood (*Casuarina* sp.) trees, but these trees are now occupied by hundreds of feral pigeons (*Columba livia*) rather than White Terns. If White Terns continue to increase on Oahu, they may spread inland, to other coasts of the island, and to other islands. White Terns have been reported on land several times on Maui, but have not been observed breeding (F. Duvall pers. comm.).

Although White Terns are tolerant of people and noise, tree trimming and construction projects should be conducted during fall and early winter when fewer White Terns are breeding, and in ways that minimize disturbance. White Terns provide an excellent educational opportunity because they are one of few native birds in Hawaii that can be seen easily by people in urban areas. White Terns nest in many schoolyards, and monitoring of their nests could be the subject of outdoor biology projects.

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SANDHILL CRANE NESTING SUCCESS AND PRODUCTIVITY IN RELATION TO PREDATOR REMOVAL IN SOUTHEASTERN OREGON

CARROLL D. LITTLEFIELD[1,2]

ABSTRACT.—I reviewed Greater Sandhill Crane (*Grus canadensis tabida*) reproductive success at Malheur National Wildlife Refuge in southeastern Oregon, 1966–1989, during which time predators were removed in 12 years and not removed in 12 years. Of 1,024 comparable crane nests found in those years, compared to those during nonremoval years, nests during years when some predators were removed had greater nesting success, more young fledged/100 pairs, lower mortality rates of young, and higher annual recruitment rates. The most important limiting factor for cranes at Malheur NWR was low annual recruitment resulting primarily from predation on eggs and prefledged young. Coyotes (*Canis latrans*) were the primary predator on eggs and young, but in some years Common Ravens (*Corvus corax*) and raccoons (*Procyon lotor*) took a large number of eggs.
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Across a wide range of habitats and geographical locations, nest predation has been recognized as the primary source of loss for many avian species, accounting for a mean of 80% of mortality (Martin 1993). This is particularly evident for species associated with wetland environments. For example, Mallard (*Anas platyrhynchos*) mortality rates in the Prairie Pothole Region of North America have ranged from 88–92% for clutches and 50–73% for prefledged young (Sargeant et al. 1993). The Sandhill Crane (*Grus canadensis*), another wetland species, frequently suffers substantial losses of nests and young in some regions of the western United States (Drewien et al. 1985, Littlefield 1995a). Although other mortality factors occur in western crane populations (especially those hunted), low annual recruitment generally is a major limiting factor (Drewien et al. 1995) and is due primarily to predation of eggs and prefledged young.

Malheur National Wildlife Refuge in southeastern Oregon hosts the greatest number of Greater Sandhill Cranes (*G. c. tabida*) breeding in the Pacific Coast states of North America (Littlefield et al. 1994). However, crane nesting and fledging success at Malheur NWR are limited by predation (Littlefield 1976, 1995a, 1995b). Coyotes (*Canis latrans*) are the primary predators of both eggs and prefledged young, but in some years raccoons (*Procyon lotor*) and Common Ravens (*Corvus corax*) take a large number of clutches (Littlefield 1976, 1995a). Other predators implicated in the mortality of young include mink (*Mustela vison*), Northern Harriers (*Circus cyaneus*), Golden Eagles (*Aquila chrysaetos*), and Great Horned Owls (*Bubo virginianus*; Littlefield and Lindstedt 1992, Ivey and Scheuering 1997). Although these four species kill some young, they generally are of little consequence when coyotes are at or above normal population levels (Littlefield and Lindstedt 1992).

Before 1972, predators were removed routinely from Malheur NWR by trapping, shooting, denning (removal of young), and chemical predicides. After 1972, predator removal was discontinued except during six years between 1982 and 1989; removal did not occur in 66% of the years between 1972 and 1989. The objective of this study was to examine the breeding records of cranes at Malheur NWR for the 24-year period, 1966–1989, to compare nesting success, mortality of young, and fledging success for years when at least some predators were lethally removed to those years when no predators were removed. Crane demographics, nesting habitat, and predator history at Malheur NWR were summarized elsewhere (Littlefield 1995a, 1995b; Littlefield and Thompson 1987).

STUDY AREA AND METHODS

Study area.—Malheur NWR (43° 16′ N, 118° 53′ W) encompasses approximately 75,000 ha of freshwater marshes, meadows,

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lakes, ponds, riparian systems, alkali sumps, and shrub-covered uplands within the lake system of the northwestern Great Basin. Mean annual precipitation is only 25.5 cm, but ample water usually is available from snow melt on adjoining mountain ranges. Silvies River and Silver Creek flow southward from the Blue Mountains and the Blitzen River flows northward from the Steens Mountain, and both drain into closed-basin Malheur Lake and Harney Lake (Silver Creek). The climate is characterized by hot, dry summers and cold winters; precipitation generally occurs as snow from late November through February and rain during May and June. The growing season is short and frost may occur during any month (Littlefield 1990).

The principle crane breeding areas at Malheur NWR are (1) adjacent to Silver Creek west and northwest of Harney Lake, (2) the shallows around Malheur Lake, and (3) the Blitzen Valley. Most pairs nest in Blitzen Valley, which extends southward from Malheur Lake for about 56 km. An interspersion of emergent vegetated marshes, open irrigated meadows, and uplands dominated by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), black greasewood (*Sarcobatus vermiculatus*), and/or Great Basin wildrye (*Elymus cinereus*) provide crane nesting and brood rearing habitats. Shrub-covered expanses and long stretches of rimrocks adjoin Malheur NWR on the eastern, southern, and western boundaries. These cattle-grazed public ranges provide habitat for coyotes, and rimrocks support breeding ravens. Raccoons were first recorded at Malheur NWR in 1950 (Littlefield 1995b), and are now found throughout the wetlands; coyotes and ravens also hunt wetland habitats extensively.

Most (>90%) cranes at Malheur NWR nest among course emergents, particularly broadfruited burreed (*Sparganium eurycarpum*) and hardstem bulrush (*Scirpus acutus*); common cattail (*Typha latifolia*) is used less frequently (Littlefield 1968, 1995b, 2001). These emergent stands usually are near meadows and subirrigated interfaces between wetlands and uplands, and also are principal foraging sites.

Data collection.—Nests usually were found by ground searching, but were occasionally located from fixed-winged aircraft or rarely from a helicopter. Nests were sampled throughout Malheur NWR, with most in the Blitzen Valley. From early April to late May, a sample of nests was assessed annually except during 1968, 1972, 1975, 1979, and 1988. Because Sandhill Cranes are philopatric (Walkinshaw 1949, Littlefield 1968, Drewien 1973), known breeding territories were searched until either an active or inactive nest was located. Thus, the traditional method, or apparent estimator for nest success (*sensu* Sargeant and Raveling 1992), was used in data analysis. For active nests, incubation stage was estimated using the flotation method (Westerskov 1950), and sites were marked with a lath placed at least 15 m from the nest. Nests were revisited after the estimated hatching dates to assess fates. Clutches abandoned, flooded, or infertile ($n = 72$) were not used in nesting success analyses. I compared nesting success during predator removal and nonremoval years using a 2×2 contingency test with Yates correction for continuity (Zar 1974).

Fledged cranes were counted at the grainfields of Malheur NWR during September. At one location where grain was not available and ground access poor, young were counted from a fixed-winged aircraft or helicopter. Because of the disturbance created by helicopters, all aerial counts eventually were made from fixed-wing aircraft. It was difficult to classify young using a noisy and rapidly moving plane (a Cessna 182 or 185). It was determined that cranes could be observed easily and little disturbed from a Piper Super Cub, which was used after 1984.

With the number of breeding pairs known, I calculated recruitment at Malheur NWR as (number of fledged young/fledged young + breeding adults) $\times$ 100. The recruitment rate estimates presented here were specifically for pairs breeding at Malheur NWR (see U.S. Fish and Wildlife Service 1978); for methods assessing recruitment for other populations see Drewien et al. (1995). I compared mortality of young and annual recruitment rate during years with and without predator removal by one-tailed *t*-tests (Zar 1974).

RESULTS

Nesting success.—No data were available on the number of coyotes removed during 1946–1971 when compound 1080 (sodium

TABLE 1. Predators removed from Malheur National Wildlife Refuge, southeastern Oregon, 1986–1989.

Species	1986	1987	1988	1989	Total
Coyote	166	460	226	226	1,078
Common Raven	44	124	102	43	313
Raccoon	11	16	12	28	67
Total	221	600	340	297	1,458

fluoroacetate) bait stations were used extensively at Malheur NWR and adjoining areas. Other predators no doubt were killed indirectly during the 26-year program. Crane nesting success was assessed for five years (1966–1971) before compound 1080 and other predicides were banned on public lands. Although few coyotes were noted during these years, those present had little difficulty locating crane nests, as most wetlands at Malheur NWR were severely degraded by chronic winter livestock grazing (Littlefield and Thompson 1987). Of 357 sampled crane clutches, 173 (48%) hatched, 168 (47%) were lost to predators (65 to ravens, 52 to coyotes, and 51 to raccoons), and 16 (4%) were lost for other reasons. Predator control ceased in February 1972, and coyotes became the most common egg predator at Malheur NWR after 1976.

Ten years later predator control was reinstituted. During 1982 and 1983, Common Ravens were removed from a 8,153-ha site, and both ravens and coyotes from a 7,976-ha site. The number of ravens removed was unknown, but the local population was substantially reduced (pers. obs.); 214 coyotes were dispatched. Overall, crane nesting success for 142 sampled nests was 69% and 70% in 1982 and 1983, respectively, up from 46% for 317 nests assessed during 1973–1981. Nesting success during 1983 was 80% at the site where both coyotes and ravens were removed; no increase occurred where only ravens were removed (Littlefield and Cornely 1997).

Low nest success again occurred in 1984 and 1985 when predators were not controlled. Of 117 clutches assessed, 47 (40%) hatched, 59 (50%) were lost to predators (38 to coyotes, 15 to ravens, and 6 to raccoons), and 11 (9%) were lost for other reasons. An intensive predator removal program was initiated in 1986 after crane pairs had declined from 236 in 1977 to 181 in 1986, with a major decline beginning in 1984 (Littlefield 1995a). The predators that were removed are listed in Table 1. A total of 163 crane clutches was sampled, of which 100 (61%) hatched, 51 (31%) were predated (33 by coyotes, 9 by ravens, and 9 by raccoons), and 12 (7%) clutches were lost for other reasons.

Nest success data were available for 10 years when predators were controlled and 9 years when they were not. For the 1,096 crane nests assessed during the study, 662 were in predator removal years (Table 2) and 434 in nonremoval years (Table 3). Excluding 72 clutches abandoned, flooded, or infertile, 1,024 were available for comparison, and

TABLE 2. Greater Sandhill Crane nesting success during predator removal years at Malheur National Wildlife Refuge, southeastern Oregon.

Year	Total clutches[a]	Hatched		Predated	
		n	%	*n*	%
1966	51	18	35	26	51
1967	59	25	42	33	56
1969	88	52	59	32	36
1970	76	34	45	38	50
1971	83	44	53	39	47
1982	81	54	67	24	30
1983	61	38	62	16	26
1986	60	40	67	16	27
1987	61	35	51	21	34
1989	42	25	60	14	53
Total	662	365	55	259	39

[a] Includes clutches lost to abandonment, flooding, and infertility.

TABLE 3. Greater Sandhill Crane nesting success during years in which predators were not removed at Malheur National Wildlife Refuge, southeastern Oregon.

Year	Total clutches[a]	Hatched		Predated	
		n	%	*n*	%
1973	49	10	20	37	76
1974	50	18	36	30	60
1976	52	35	67	16	31
1977	50	23	46	26	52
1978	55	19	34	24	44
1980	30	16	53	11	37
1981	31	15	48	14	45
1984	67	23	34	34	51
1985	50	24	48	25	50
Total	434	183	42	217	50

[a] Includes clutches also lost to abandonment, flooding, and infertility.

TABLE 4. Greater Sandhill Crane productivity during predator removal years at Malheur National Wildlife Refuge, southeastern Oregon.

Year	Number of breeding pairs	Mortality of young (%)	Recruitment (%)	Number of young fledged per 100 pairs
1970[a]	235	66.5	12.6	28.9
1971	(235)	80.7	8.9	19.6
1982[a]	214	90.1	5.5	11.7
1983	(214)	84.8	8.4	18.2
1986[a]	181	77.6	12.1	27.6
1987	(181)	78.4	10.6	23.7
1988	(181)	—	1.6	3.1
1989[a]	168	74.7	12.7	25.0
Mean	201	78.9	9.1	19.7
SD	26.6	7.5	3.9	8.1

[a] Years when crane pairs were counted; number of breeding pairs in the years following a count was estimated to be the same and is presented in parentheses.

nesting success was greater in years when predators were removed ($\chi^2 = 15.84$, df = 1, $P < 0.010$). With predator removal, coyotes still destroyed 17% ($n = 108$) of the clutches, compared to 27% ($n = 106$) during nonremoval years. Common Ravens destroyed 6% fewer clutches (14% versus 20%) in removal years, whereas raccoons took a slightly greater percentage (11% versus 8%). Fewer raccoons seemed present at Malheur NWR when coyotes were abundant (Littlefield 1995b).

Fledging success.—With or without predator removal, the mortality rate of young cranes was high, ranging from 66.5% in 1970 to 98.8% in 1974 (mean = 84.4%, SD = 9.4). The mortality rate of young was significantly lower in years when predators were removed ($t = -3.38$, df = 6, $P < 0.010$), and recruitment rates were significantly higher ($t = 2.90$, df = 7, $P < 0.025$). With removal, excluding the extreme drought year of 1988 when recruitment was only 1.6%, rates ranged from 5.5% in 1982 to 12.7% in 1989 (mean = 9.1%, SD = 3.9; Table 4). However, without removal, the lowest rates were 0.4% in 1973 and 1974, and the highest was 9.1% in 1976 (mean = 5.1%, SD = 3.3; Table 5). With predator removal, the number of young fledged/100 pairs ranged from 3.1 in 1988 to 28.9 in 1970 (mean = 19.7, SD = 8.1; Table

TABLE 5. Greater Sandhill Crane productivity during years in which predators were not removed at Malheur National Wildlife Refuge, southeastern Oregon.

Year	Number of breeding pairs	Mortality of young (%)	Recruitment (%)	Number of young fledged per 100 pairs
1972	(235)	—	8.4	18.3
1973	(235)	98.0	0.4	0.8
1974	(235)	98.8	0.4	0.8
1975[a]	236	—	3.5	7.2
1976	(236)	84.6	9.1	19.9
1977[a]	219	85.5	5.4	11.4
1978	(219)	70.1	8.9	19.6
1979	(219)	—	8.2	17.8
1980[a]	221	84.9	7.1	15.5
1981	(221)	88.7	5.0	10.5
1984	(214)	93.9	1.8	3.7
1985[a]	186	92.6	2.4	4.8
Mean	224	88.6	5.1	10.9
SD	15	8.8	3.3	7.3

[a] Years when crane pairs were counted; number of breeding pairs in the years following a count was estimated to be the same and is presented in parentheses.

4). When predator numbers were not reduced, the range was 0.8 in 1973 and 1974 to 19.9 in 1976 (mean = 10.9, SD = 7.3; Table 5).

DISCUSSION

From 1966–1989, during 12 years when predator numbers were reduced, a mean of 55% of Sandhill Crane clutches hatched at least one egg, compared to 42% in years lacking predator removal. For 19 years when nesting success was assessed, coyotes were the most important predator, taking 214 (22%) of 1,024 clutches, although raccoons were the major egg predator in 1967 and 1969. There was little evidence that raccoons were eruptive (*sensu* Fritzell 1982), and increased raccoon predation rates corresponded with years when coyote numbers were below normal (Littlefield 1995b). High coyote density may impact raccoon density (Greenwood and Sovada 1996) or activity. Common Ravens were responsible for taking the greatest number of clutches during 1970, 1971, and 1973. Except for 1973, more raccoon and raven predation occurred when coyotes were being intensively controlled throughout the western United States with the predicide compound 1080.

Unlike other wetland birds, cranes differ in brood-rearing behavior and brood habitat use. Pairs generally nest in aquatic situations, but move their young to nearby uplands, meadows, and moist ecotones for rearing. These sites also are the principal foraging areas for most mammalian predators. Greater Sandhill Crane young require 66–75 days to fledge and are highly vulnerable to predation. Telemetry studies at Malheur NWR during the mid-1980s found 68% of 25 monitored flightless young were lost to predators; coyotes consumed 52% with one or two known losses attributed each to raccoons, domestic dogs, or Great Horned Owls (Littlefield and Lindstedt 1992). Ravens, however, have not been observed preying on young cranes at Malheur NWR.

Two of the most important predators, ravens and coyotes, have increased substantially since the early 1970s. Throughout North America there was significant raven population growth between 1965 and 1979, particularly in the California foothills and Rocky Mountain states (Robbins et al. 1986). During 1980–1994, ravens increased at annual rates of 5.8% in Oregon and 6.8% in Washington (Sharp 1996). After predicide restrictions on public lands in 1972, coyote populations markedly increased in the Pacific Northwest, especially in the shrub-steppe region of southeastern Oregon (Willis et al. 1993). Coyote population growth was not restricted to the Pacific Northwest, e.g., increases also were noted in southeastern Idaho (Drewien et al. 1985), northeastern California, and on the southern High Plains of northwestern Texas (pers. obs.). Since the 1970s, the species also has been expanding and reoccupying former ranges in the Prairie Pothole Region of the northern Great Plains (Sovada et al. 1995), suggesting widespread population growth throughout western North America.

The gray wolf (*C. lupus*), which generally excludes or preys upon coyotes (Carbyn 1982), has been eradicated over most of its historical western range, and the coyote has become and will perhaps continue to be the top carnivore. Public sentiment likely will limit wolf reintroductions and restrict coyote control methods. Commercial fur harvest may be the only means available for coyote population management. With modification of harvest regulations, coyote numbers probably will continue to increase in the Prairie Pothole Region and, along with subsequent interspecific canid exclusion, reduce red fox (*Vulpes vulpes*) populations; foxes in the northern prairies currently are an important predator of breeding adult waterfowl and their nests (Sovada et al. 1995). Few cranes breed in the prairie region, except in northwestern Minnesota, but if coyote numbers substantially increase, management will be warranted to ensure the species does not become overly abundant. It will be important to evaluate the entire avian community of an area before decisions are made on which canid predator is to be encouraged, managed, or protected. Otherwise, more problems may arise than are resolved, especially if coyotes become as abundant and destructive on nesting cranes as they presently are in some regions of the Rocky Mountains and Great Basin. This will be particularly important for the few wetlands in the northern prairies which support breeding Sandhill Cranes.

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ARE RESULTS OF ARTIFICIAL NEST EXPERIMENTS A VALID INDICATOR OF SUCCESS OF NATURAL NESTS?

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ABSTRACT.—Studies using artificial nests to assess rates or patterns of nest predation have increased during recent decades. However, the critical assumption that temporal or spatial patterns of relative predation rates of artificial nests parallel those of natural nests has begun to be questioned. We compared the daily survival rate for 365 artificial nests with that estimated for 295 open nests of passerines, and analyzed the trends in survival rates for both nest types among three breeding seasons and three species of nest plants in the central Monte Desert, Argentina. Daily survival rate for artificial nests (0.737) was significantly lower than that for natural nests (0.925). Trends in survival rates of artificial nests over years and among species of nest plants only partially reflected those of natural nests. Our results support the well established finding that artificial nests may not accurately estimate actual rates of nest predation. Artificial nests may provide an additional source of data to natural nests when testing ecological hypotheses, but artificial nest experiments should be carefully designed (i.e., realistic) and should attempt to identify predators of artificial and natural nests to validate the experimental results. *Received 24 October 2002, accepted 10 March 2003.*

The main cause of nest mortality in most bird species is predation (Ricklefs 1969, Rotenberry and Wiens 1989, Martin 1993, Mezquida and Marone 2001). However, it often is difficult to obtain the appropriate number of natural nests to assess different factors influencing rates of nest predation (Reitsma et al. 1990). For this reason, the use of artificial nests to estimate nest predation rate has increased during the last few decades (reviewed in Major and Kendal 1996, Sieving and Willson 1998, Schmidt and Whelan 1999). Major and Kendal (1996) summarized the diverse, and sometimes nonrigorous, field techniques used in these types of experiments that at times make analysis of pattern consistency difficult.

Absolute rates of predation on artificial nests commonly have been found to differ from those of natural nests. Some authors have found similar predation rates in artificial and natural nests (see references in Major and Kendal 1996), but most studies have shown either lower predation pressure for natural compared to artificial nests (Bechet et al. 1998, Sloan et al. 1998, Wilson et al. 1998, Zanette 2002) or more intense predation on natural nests (Chamberlain et al. 1995, Davison and Bollinger 2000). However, this is not necessarily a problem for comparative studies on artificial nests. Despite the fact that absolute predation rates may differ between natural and artificial nests, inferences derived from artificial nests can be valid if relative predation rates follow a similar and consistent trend in both types of nests. This assertion, commonly used to justify the artificial approach, usually has not been tested and the results at hand are conflicting. In some studies, rates of predation for both nest types did not follow the same pattern (Willebrand and Marcstrom 1988, MacIvor et al. 1990, Buler and Hamilton 2000), while trends were similar for artificial and natural nests in other studies (George 1987, Ammon and Stacey 1997, Wilson et al. 1998). Moreover, when a series of treatments was considered in the study (e.g., types of artificial nests, spatial and temporal variations), the relationship between the success of artificial and real nests usually differed among subsets of data (Butler and Rotella 1998, Davison and Bollinger 2000, Weidinger 2001a, Zanette 2002).

In this study, we examined whether predation on artificial nests reflects that of natural nests of passerines in an area of southern South America. We compare absolute rates of predation of artificial and natural nests. We also compare trends in predation rates for ar-

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TABLE 1. Nests of 15 species of open-nesting passerines from Ñacuñán made up the sample of natural nests used for survival rate calculations.

Species	Number of nests
Ringed Warbling-Finch, *Poospiza torquata*	95
Gray-crowned Tyrannulet, *Serpophaga griseiceps*	74
Cinnamon Warbling-Finch, *Poospiza ornata*	53
Greater Wagtail-Tyrant, *Stigmatura budytoides*	18
Many-colored Chaco-Finch, *Saltatricula multicolor*	16
Crowned Slaty-Flycatcher, *Empidonomus aurantioatrocristatus*	12
White-banded Mockingbird, *Mimus triurus*	11
Black-crowned Monjita, *Xolmis coronata*	4
Scrub Flycatcher, *Sublegatus modestus*	4
Golden-billed Saltator, *Saltator aurantiirostris*	2
Yellow-billed Tit-Tyrant, *Anairetes flavirostris*	2
Fork-tailed Flycatcher, *Tyrannus savana*	1
Rufous-collared Sparrow, *Zonotrichia capensis*	1
Vermilion Flycatcher, *Pyrocephalus rubinus*	1
White-tipped Plantcutter, *Phytotoma rutila*	1
Total	295

tificial and natural nests both temporally (across three breeding seasons) and spatially (across three species of nest plants), and discuss the validity of using trends observed in artificial nests to infer trends in natural nests.

METHODS

We conducted this study in the Biosphere Reserve of Ñacuñan (34° 03′ S, 67° 54′ W), Mendoza province, Argentina. The reserve is located in an alluvial plain of the central Monte Desert and comprises an open *algarrobo* (*Prosopis flexuosa*) woodland with scattered chañar trees (*Geoffroea decorticans*), abundant tall shrubs >1 m tall (*Larrea divaricata*, *Capparis atamisquea*, *Atriplex lampa*), low shrubs <1 m tall (mainly *Lycium* spp.), and perennial grasses (*Pappophorum* spp., *Trichloris crinita*, *Setaria leucopila*, *Digitaria californica*, *Aristida mendocina*). Annual forb cover is highly variable from year to year and usually lower than grass cover. The climate of Ñacuñan is dry and temperate, with cold winters. Most precipitation (78% of annual rainfall) occurs during the spring and summer months (October to March; Marone et al. 2000).

Birds such as the Chimango Caracara (*Milvago chimango*) and Brown Cacholote (*Pseudoseisura lophotes*) appear to be the most important nest predators in the reserve, although some mammals such as the small fat-tailed opossum (*Thylamys pusilla*, Didelphidae) and the little grison (*Galictis cuja*, Mustelidae) also have been confirmed as nest predators (Mezquida and Marone 2002). Other potential predators include the white-eared opossum (*Didelphis albiventris*, Didelphidae), Molina's hog-nosed skunk (*Conepatus chinga*, Mustelidae), South American grey fox (*Dusicyon griseus*, Canidae), and small snakes.

Natural nests.—During spring and summer (October to March) from 1996–1997 to 1998–1999 (i.e., three breeding seasons), we located open nests of passerines by systematic searches in the vegetation and by following adult birds (Martin and Geupel 1993). Most nests were placed in chañar and zampa (*Atriplex lampa*), two plant species widely used for nesting in this area (Mezquida and Marone 2001). All nests included in our sample of natural nests (see Table 1) were found in the shrub-midstory (≤1.5 m) or canopy-subcanopy (>1.5 m) strata. Nests placed in these two strata showed similar survival rates (Mezquida 2000). Each nest was visited every 1–3 days until it either failed or fledged young. Nests that fledged at least one young were considered successful. A nest was considered depredated when all the eggs or young nestlings disappeared (see Mezquida and Marone 2001 for further details).

Artificial nests.—Concurrent with our studies of natural nests, we conducted artificial

nest experiments. In the open woodland habitat, we established two or three divergent transects (≥200 m apart at origin) along scarcely used tracks inside the reserve. On each transect, we tied small pieces of colored tape to vegetation, alternating on the right and left side of the track, at 40–50 m intervals. One nest was placed more than 20 m from each mark in a perpendicular direction to the transect. To aid in locating nests again, we tied a new mark to the vegetation, in most (>80%) cases >10 m from the nest, following suggestions by Major and Kendal (1996). Artificial nests were open cup natural nests collected during the previous breeding season, mainly Ringed Warbling-Finch (*Poospiza torquata*) and Cinnamon Warbling-Finch (*P. ornata*) nests. All of the nests we used in the experiments were small cups made of grasses with an external diameter of 6–7 cm and an external height of 5–6 cm. We placed the nests in three plant species, chañar, jarilla (*Larrea* spp.), and zampa, trying to imitate natural positions. Range of nest heights in each plant were 1–2 m (chañar), 0.5–1.0 m (jarilla), and 0.5–1.0 m (zampa). Each nest was baited with two fresh quail (*Coturnix* sp.) eggs. Quail eggs are bigger than those of the local passerines. However, the use of these eggs in our experiments does not appear to have biased our results (see Discussion). Total exposure period was 12 days for each experiment, similar to the mean incubation period of the passerine assembly breeding in the area (Mezquida and Marone 2001). We checked the nests every two days taking care to approach the nests from different directions to avoid creating obvious paths for potential predators. When we detected the presence of a potential predator, we did not approach the nest until the predator moved away. Artificial nests with both eggs missing or damaged were classified as depredated. Therefore, nests with one or both eggs undamaged at the end of the experiment were considered successful. Artificial nests and eggs were removed when the nest was considered depredated or after the exposure interval if survival occurred.

Analyses.—We calculated the daily survival rate of natural and artificial nests using the Mayfield method (Mayfield 1975), and its associated variance (Johnson 1979). For natural nests, we included only nest mortality caused by predation and using this, we calculated daily predation rate (m_p). Daily survival rate to predation (s_p) was equal to $1 - m_p$. We estimated total exposure days as the interval between the day when the nest was found active (i.e., with eggs or nestlings) and the fledging of the young or halfway between the two subsequent visits between which a nest failed. We counted total exposure days for artificial nests in a similar way. Nest mortality (mainly due to predation) for natural nests was very high during our study (usually <80%; Mezquida and Marone 2001). Therefore, to increase sample size and the confidence of survival rate estimates, we calculated the daily survival rate of natural nests during the egg and nestling period as a whole, because daily survival rates did not differ significantly between the two stages (Mezquida and Marone 2001). We used the Hensler and Nichols (1981) test to test for differences in daily survival rate between artificial and natural nests. We compared daily survival rates for artificial and natural nests among years and nest plants using methods described by Aebischer (1999). We tested the goodness-of-fit of different models for each two-way comparison (i.e., nest type × year and nest type × nest plant) and used likelihood-ratio tests for comparisons between models.

RESULTS

We distributed 365 artificial nests in the open woodland, 353 of which were depredated during 1,344 exposure days. The sample of natural nests included 295 nests of 15 bird species, although most (95%) nests were of the seven most numerous species (with more than 10 nests each; Table 1). During a total of 2,628.5 exposure days, 197 natural nests failed due to predation. The resulting daily survival rates were significantly lower for artificial nests (daily survival probability ± associated variance = $0.737 \pm 1.4 \times 10^{-4}$) than for natural nests ($0.925 \pm 2.6 \times 10^{-5}$; Hensler and Nichols test, $Z = 14.4$, $P < 0.0001$).

The full model that included the main effects of nest type, year, and the interaction between them (deviance = 567.5, df = 654, $P = 0.99$) fitted well. The comparison of the full model with a model with main effects only (deviance = 1378.3, df = 656) showed that there was a significant interaction between

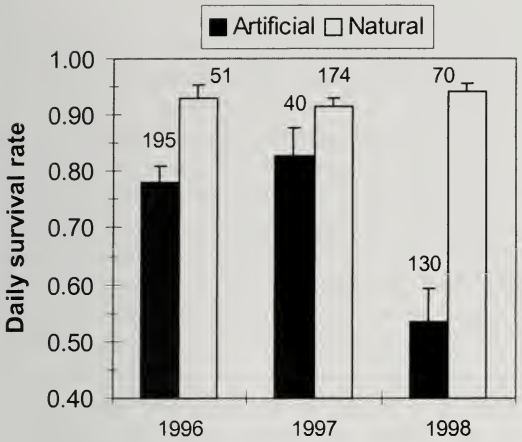

FIG. 1. Daily survival rates of artificial nests were always lower than those of natural nests during the three years studied, but was especially low for artificial nests during 1998. Daily survival rates, 95% confidence ranges (Hensler and Nichols 1981) and number of nests are shown for artificial and natural nests during three breeding seasons (austral spring and summer) in the Reserve of Ñacuñan, Argentina.

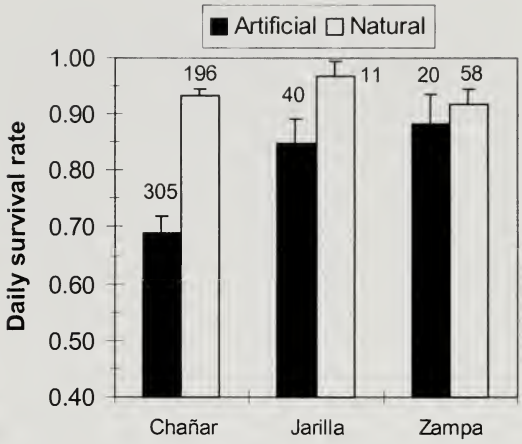

FIG. 2. Daily survival rates of artificial nests were consistently lower than those of natural nests in all nest plants, but the relative rate for artificial nests placed in zampa was higher than that of natural nests. Thus, both nests types showed nonparallel trends. Bars represent the daily survival rate and the 95% confidence range of each nest type in three plant species at Ñacuñan, Argentina. Sample sizes are indicated for each group.

nest type and year ($D = 810.8$, df = 2, $P < 0.0001$). A model that included the main effect of nest type (deviance = 610.0, df = 658, $P = 0.91$) showed a good fit, whereas a model with just temporal effects was rejected (deviance = 768.2, df = 657, $P = 0.002$). Thus, the daily survival rate of artificial nests was consistently lower compared to natural nests, but was particularly low during 1998, causing an interaction between nest type and year (Fig. 1).

Similarly, a full two-way model with interactions to examine the effect of nest type and species of nest plant on daily survival rates showed a satisfactory fit (deviance = 535.6, df = 624, $P = 1.00$). The likelihood-ratio test that compared the full model with a two-way model without interactions (deviance = 1306.9, df = 626) was significant ($D = 771.4$, df = 2, $P < 0.0001$), indicating a significant nest type × nest plant interaction. A model specifying just nest type effects (deviance = 569.5, df = 628, $P = 0.95$) showed a good fit, whereas a model with just nest plant effects (737.4, df = 627, $P = 0.002$) fitted poorly. The daily survival rates were lower for artificial nests in all nest plants, but increased from chañar to zampa, whereas the daily survival rates of natural nests in chañar and zampa were lower than that in jarilla (Fig. 2).

DISCUSSION

Our results, in agreement with other findings, showed that artificial nests suffered higher predation pressure than natural nests (Sloan et al. 1998, Wilson et al. 1998, Zanette and Jenkins 2000). However, this is not surprising because most studies comparing absolute rates of predation between artificial and natural nests have found differences. Many factors might explain the discrepancy in the probability of every nest type being predated (reviewed in Major and Kendal 1996). Although studies designed for one or a small number of bird species could better simulate natural conditions, our artificial nests were reasonably realistic. We did not use artificial structures (e.g., wire baskets, tennis balls) to simulate nests, but natural nests in order to avoid artificial biases (Martin 1987). Further, we placed the nests in plants and positions based on previous knowledge of the nesting ecology of local passerines in the study area.

In contrast, the use of quail eggs in the artificial nests might justify some criticism suggesting that our predation rate estimates are biased. The size of quail eggs (mean length:

32.7 mm, $n = 60$) was larger than the mean egg size for bird species included in the sample of natural nests (19.9 mm, $n = 15$ species; Mezquida 2000), which could have increased the detectability of eggs in artificial nests. However, some small-mouthed nest predators are unable to break quail eggs (Roper 1992, Haskell 1995), and others do not appear to consume this type of egg (Marini and Melo 1998). Hence, the use of commercially available eggs might under- as well as overestimate predation rate on artificial nests. The results of specific experiments conducted at the Reserve of Ñacuñan suggested that this potential bias was a minor one; the predation rate for artificial nests baited with eggs that more accurately resembled eggs of the local passerine species was similar to the predation rate for nests baited with quail eggs (Quse 2001). The pattern of egg coloration also differed between quail and natural eggs, although previous studies indicate that egg color does not seem to affect predation rate (Jobin and Picman 1997, Weidinger 2001b).

Even though results of experiments using artificial nests do not generally offer realistic indicators of actual nest predation, this might not invalidate their use if patterns or trends (i.e., relative rates of predation) among treatments are similar in both nature and experiments. However, studies comparing the success of artificial and natural nests in different treatments (e.g., habitats, patches, years) have obtained conflicting results, as in the present study. Our results show that patterns of predation of artificial nests across years and species of nest plants did not closely parallel those found for natural nests. In our first comparison, the survival rate of artificial nests during the first two breeding seasons followed the same trend as in natural nests, but the pattern differed during the next breeding season. The decreased survival rate of artificial nests over time might be a consequence of predators learning to find artificial eggs (Major and Kendal 1996, Vander Haegen and DeGraaf 1996). For example, Buler and Hamilton (2000) also observed an increase in predation of artificial nests between two consecutive years, contrary to predation of natural nests, and suggested the potential for learning by predators (mainly crows). In Ñacuñan, we did not use the same transects for later trials, but we used the same general area to place artificial nests in successive years, probably facilitating predators to learn to detect our proffered nests.

Another comparison showed that the survival rate of artificial and natural nests differed depending upon the species of plant that supported the nest, but patterns were not fully similar for both nest types. The survival rate of artificial nests was lowest in chañar and highest in zampa. Chañares are small trees with small and dispersed leaves, while zampas are medium-sized and compact shrubs with abundant evergreen leaves. Thus, the pattern of predation on artificial nests suggests that the degree of nest concealment might have played a role. Moreover, birds appear to be major nest predators at our study area (Mezquida and Marone 2002), and these visual predators probably were very efficient at detecting our artificial nests, mainly those placed in chañar that were higher and less concealed. Other studies also have suggested that the degree of concealment is an important factor that affects success of nests unattended by parents (Götmark et al. 1995, Major and Kendal 1996, Cresswell 1997). Natural nests also suffered high predation pressure, but rates for nests built in chañar and zampa were similar. In contrast to artificial nests, the relative incidence of terrestrial predators (i.e., mammals and reptiles) on natural nests in zampa presumably would be higher, due to the presence of parents and the activity at the nests (Davison and Bollinger 2000).

In conclusion, our results for a location of central-western Argentina add new evidence to the well established pattern that artificial nests are not always a trustworthy indicator of predation rates on natural nests. Whether absolute rates of predation on artificial nests are higher or lower than those on natural nests probably depends upon characteristics of the artificial setup (e.g., nest site and position, nest type) and the kind of predators involved. Our study also showed that temporal and spatial trends in daily survival rates of artificial nests did not closely correspond with those of natural nests. Differences suggest behavioral responses by predators and that, at least in some situations, both types of nests may not attract the same predators. We recommend that future studies using artificial nests should

be realistic (i.e., based on the nesting ecology of the target species) and concurrent with a study on natural nests, and should attempt to identify predators of both nest types to validate the experimental results. In addition to natural nest experiments, carefully designed artificial nest experiments may provide an independent source of data (i.e., a measure of potential predation pressure) that help explain how avian species may be adjusting to different predation pressures (Sieving and Willson 1998).

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PATTERNS OF COWBIRD PARASITISM IN THE SOUTHERN ATLANTIC COASTAL PLAIN AND PIEDMONT

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ABSTRACT.—Until recently, little information was available on patterns of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) in the southeastern United States, a region into which cowbirds expanded their range only during the last half of the Twentieth Century and where their abundance is relatively low. We compiled parasitism data from several published and unpublished studies conducted in Georgia and South Carolina from 1993–2000 to examine levels of brood parasitism and determine frequent host species. The combined dataset included 1,372 nests of 24 species reported in the literature to have been parasitized by cowbirds. The parasitism rate on all species combined was 8.2%. Considering only those species that served as hosts in these studies (n = 12), the parasitism rate was 9.3%. Seven species were parasitized at rates ≥10%. Based on the extent of parasitism (among studies and locations), their relative abundance, and the sample size of nests, Prairie Warblers (*Dendroica discolor*), Hooded Warblers (*Wilsonia citrina*), Yellow-breasted Chats (*Icteria virens*), and Indigo Buntings (*Passerina cyanea*), all shrub nesters, appear to be the most important cowbird hosts in the region. Parasitism on some species reported as frequent hosts elsewhere was extremely low or not documented. We conclude that the impact of brood parasitism on the seasonal fecundity of hosts in the region probably is minimal, but additional work is warranted on species of concern, such as the Painted Bunting (*Passerina ciris*). *Received 3 April 2003, accepted 26 July 2003.*

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) has been studied intensively in many parts of their range, particularly near the center of their historical range in the midwestern United States (Lowther 1993). Levels of cowbird parasitism vary markedly according to region (Hoover and Brittingham 1993), landscape (Robinson et al. 1995), and habitat (Brittingham and Temple 1996, Burhans 1997). For example, parasitism rates on Wood Thrushes (*Hylocichla mustelina*) range as high as 100% in some Midwestern host populations (Robinson et al. 1995), but rates can be <10% within the same region and in northeastern populations (Roth et al. 1996). Parasitism typically results in a reduction in the number of host young fledged per nesting attempt, but the effect of various levels of parasitism on seasonal productivity of hosts is less clear (Pease and Grzybowski 1995). Although recent evidence suggests that the impacts of parasitism on seasonal fecundity may be minimal in some situations (Schmidt and Whelan 1999, Whitehead et al. 2000), cowbirds still are widely considered a negative influence on those host species that are declining.

The Brown-headed Cowbird colonized the southeastern United States during the first half of the Twentieth Century and did not reach the southeastern Coastal Plain until after 1957 (Cruz et al. 2000). Although the species increased in the southeastern Coastal Plain between 1970 and 1988 (Wiedenfeld 2000), it declined from 1988–2002 in the three southeastern Breeding Bird Survey (BBS) regions (Southern Piedmont, Upper Coastal Plain, and Coastal Flatwoods; Sauer et al. 2003). Cowbird abundance throughout most of Georgia and South Carolina currently is low relative to the rest of the species' range; during the period 1982–1996, a mean of 4–10 birds were detected per BBS route compared to 11–100 birds throughout most of the Midwest and Great Plains and >100 in the area of greatest abundance in North Dakota (Sauer et al. 2003). Cowbird abundance in the southeastern United States probably is limited by landscape structure, as the region is among the most heavily forested in the eastern United States, with 65–74% of the land area classified as timberland (Trani et al. 2001).

In spite of the Brown-headed Cowbird's increase in population size and range expansion into this area of naive hosts, until recently there has been little information published on cowbird parasitism patterns in the Southeast,

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TABLE 1. Number of nests of species that regularly host Brown-headed Cowbirds (range-wide) and number of species represented from studies reporting parasitism at each of four study sites in Georgia and South Carolina, 1993–2000.

Location	Number of nests	Species	Study
Fort Benning Military Reservation	266	7	Howell (1998)
Piedmont National Wildlife Refuge	474	20	Brunjes (1998), Raftovitch (1998), Lang (1998), White et al. (1999), L. A. Powell (unpubl. data)
Savannah River Site	411	21	Sargent et al. (1997, 2003, unpubl. data), Moorman (1999, unpubl. data), Moorman et al. (2002), Krementz and Powell (2000), Stober and Krementz (2000), P. J. Champlin and JCK (unpubl. data)
James Island	261	6	Whitehead et al. (2000)

perhaps in part because of the low relative abundance of cowbirds in the region. Nevertheless, considerable interest exists among land managers and researchers as to the risks posed by cowbird parasitism to songbird populations. To examine levels and patterns of cowbird parasitism in the southern Atlantic Coastal Plain and adjacent Piedmont, we present data compiled from unpublished and recently published songbird nesting studies conducted during the 1990s and 2000 at four locations in Georgia and South Carolina.

STUDY AREAS AND METHODS

We compiled data from published and unpublished studies (Table 1) conducted at four locations across the Piedmont and southern Atlantic Coastal Plain physiographic provinces in Georgia and South Carolina:

Fort Benning Military Reservation.—Howell (1998) monitored nests from 1995–1996 at Fort Benning (32° 39′ N, 84° 82′ W), located on the Fall Line dividing the Piedmont and Coastal Plain physiographic provinces in western Georgia. Approximately 65% of the site is pine (*Pinus* spp.) forest, with the remainder in mixed pine-hardwood and bottomland hardwood forests. Study sites were in 26- to 104-year-old pine forests managed for Red-cockaded Woodpeckers (*Picoides borealis*; Howell 1998).

Piedmont National Wildlife Refuge.—Several workers (Brunjes 1998, Lang 1998, Raftovitch 1998, White et al. 1999, L. A. Powell unpubl. data) monitored nests from 1993–1997 at Piedmont NWR (33° 11′ N, 83° 77′ W) in the Piedmont physiographic province of central Georgia. The site is dominated by pine and mixed pine-hardwood forest, with pure hardwood forests confined to small drainages (Brunjes 1998). Study sites were in pine and mixed pine-hardwood forests ≥60 years old.

Savannah River Site.—Several workers (Sargent et al. 1997, 2003, unpubl. data; Moorman 1999, unpubl. data; Krementz and Powell 2000; Stober and Krementz 2000; Moorman et al. 2002; P. J. Champlin and JCK unpubl. data) monitored nests from 1993–2000 at the Savannah River Site (33° 28′ N, 81° 67′ W). This site is a U.S. Dept. of Energy National Environmental Research Park in the Upper Coastal Plain physiographic province in western South Carolina. Approximately 62% of the site is <80-year-old pine forest, 20% is 50- to 100-year-old bottomland hardwood forest, and the remainder is 50- to 100-year-old upland hardwood and mixed pine-hardwood forest. Approximately 10% was in <10-year-old pine plantation (Blake in press).

James Island, South Carolina.—Whitehead et al. (2000) monitored nests from 1997–1998 at James Island (32° 73′ N, 79° 96′ W), a coastal barrier island near Charleston, South Carolina. Study sites were old fields composed of 4- to 8-year-old successional vegetation. Fields were surrounded by mixed pine-hardwood forest (Whitehead et al. 2000).

The landscape composition and context of the study sites, which were more forested than the areas surrounding them, may have biased the observed parasitism rates slightly downward relative to the region. However, we believe the reported parasitism rates are approximately representative of the region as a whole

for the following reasons. First, the landscape of Georgia and South Carolina is primarily forested (Trani et al. 2001). Second, all study sites were accessible to cowbirds; one entire site (James Island) and portions of the remaining three were within the commuting range of cowbirds from high quality foraging areas (7 km; Rothstein et al. 1984, Thompson 1994), and cowbirds were observed throughout each site (J. H. Brunjes pers. comm., M. A. Howell pers. comm., JCK pers. obs., M. A. Whitehead pers. comm.). Finally, one of the sites, James Island, was in a landscape predominantly fragmented by suburban development.

During all studies nests were located and nesting success was monitored according to standard protocols (Martin and Geupel 1993). Here, we consider only those species that regularly host cowbirds (Friedmann 1963, Friedmann and Kiff 1985). We identify frequent hosts as those with regional parasitism rates ≥10%.

RESULTS AND DISCUSSION

The combined dataset included 1,372 nests of 24 species (Table 1). Each study site was represented by at least 260 nests of potential host species. Additional nest data existed among the reported studies for several species known to have hosted cowbirds (Friedmann 1963, Friedmann and Kiff 1985), but which are either seldom parasitized or reject cowbird eggs when parasitized (i.e., they rarely raise cowbird young successfully). These included Mourning Doves (*Zenaida macroura*, $n = 4$), Yellow-billed Cuckoos (*Coccyzus americanus*, $n = 18$), Northern Mockingbirds (*Mimus polyglottos*, $n = 2$), and Brown Thrashers (*Toxostoma rufum*, $n = 16$). None of these were parasitized in the reported studies.

Of the 1,372 nests, only 113 (8.2%) were parasitized, and of the 24 potential hosts, only 12 actually served as hosts (Table 2). The parasitism rate on 1,212 nests of actual hosts was 9.3%. Seven species were frequent hosts (total parasitism rates ≥10%): White-eyed Vireos (*Vireo griseus*), Prairie Warblers (*Dendroica discolor*), Hooded Warblers (*Wilsonia citrina*), Yellow-breasted Chats (*Icteria virens*), Indigo Buntings (*Passerina cyanea*), Painted Buntings (*P. ciris*), and Blue Grosbeaks (*Guiraca caerulea*). Among these species, the mean parasitism rate was 18.2%. Considering the extent of parasitism (among studies and locations), the abundance of the hosts, and sample sizes of nests, Prairie Warblers, Hooded Warblers, Yellow-breasted Chats, and Indigo Buntings appeared to be the most important cowbird hosts in the region. The mean parasitism rate on these species was 15.8%.

The suite of species parasitized most frequently differed somewhat from that reported by Friedmann (1963; see also Lowther 1993) for the entire range of the cowbird, and from Potter and Whitehurst (1981) for the Carolinas. Only two (Yellow-breasted Chats and Indigo Buntings) of the seven frequent hosts reported here are among the 17 most frequent cowbird hosts range-wide (Friedmann 1963), despite several of those species being well represented in our sample. In contrast, White-eyed Vireos, Prairie Warblers, and Hooded Warblers were frequent hosts in Georgia and South Carolina, but are not among the 17 listed by Friedmann (1963), though all three are well-known cowbird hosts (Hopp et al. 1995, Nolan 1978, Evans Ogden and Stutchbury 1994, respectively). Species that frequently host cowbirds elsewhere (Lowther 1993, Roth et al. 1996) but rarely did in these studies included Wood Thrushes (2 of 169), Ovenbirds (0 of 11), Kentucky Warblers (*Oporornis formosus*; 0 of 33), and Eastern Towhees (*Pipilo erythrophthalmus*; 4 of 109; Table 2). Potter and Whitehurst (1981) reported that Eastern Towhees were the most frequent host and Wood Thrushes were the fourth most frequent host in the Carolinas. These authors reported only single observations of parasitism each for White-eyed Vireos, Prairie Warblers, Yellow-breasted Chats, Indigo Buntings, and Painted Buntings, and no observations for Hooded Warblers. However, their data consisted primarily of observations of adults feeding fledglings in backyard habitats, where Eastern Towhees and Wood Thrushes may be more likely to appear than the frequent hosts.

All seven frequent hosts are understory nesters, with six (White-eyed Vireos, Prairie Warblers, Yellow-breasted Chats, Indigo Buntings, Painted Buntings, and Blue Grosbeaks) using shrub-scrub habitats and one (Hooded Warblers) using bottomland hardwood forests. Although canopy-nesting species generally were under represented in the sample, ground

TABLE 2. Rates of brood parasitism by Brown-headed Cowbirds in Georgia (Piedmont National Wildlife Refuge, PNWR; Fort Benning Military Reservation, FBMR) and South Carolina (Savannah River Site, SRS; James Island, JISC) from 1993–2000. All species listed are known cowbird hosts (Friedmann 1963, Friedmann and Kiff 1985).

Species	Site	Relative abundance[a]	Number of nests	Number parasitized	Percent	Source
Acadian Flycatcher (*Empidonax virescens*)	SRS	C	3	0	0	Moorman (1999), R. A. Sargent et al. (unpubl.)
	PNWR	U	1	0	0	Brunjes (1998), Raftovitch (1998)
Total			4	0	0	
White-eyed Vireo (*Vireo griseus*)	PNWR	C	2	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	C	18	2	11.1	Moorman (1999), R. A. Sargent et al. (unpubl.)
Total			20	2	10.0	
Blue-headed Vireo (*Vireo solitarius*)	PNWR	R	7	0	0	Brunjes (1998), Raftovitch (1998)
Red-eyed Vireo (*Vireo olivaceous*)	PNWR	C	5	0	0	Brunjes (1998), Raftovitch (1998)
Carolina Wren (*Thryothorus ludovicianus*)	PNWR	V	1	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	V	17	0	0	Moorman (1999, unpubl.), R. A. Sargent et al. (unpubl.)
Total			18	0	0	
Blue-gray Gnatcatcher (*Polioptila caerulea*)	PNWR	C	2	0	0	Brunjes (1998), Raftovitch (1998)
Wood Thrush (*Hylocichla mustelina*)	PNWR	C	143	2	1.4	Brunjes (1998), Lang (1998), Raftovitch (1998), L. A. Powell (unpubl.)
	SRS	C	26	0	0	Sargent et al. (2003)
Total			169	2	1.2	
Prairie Warbler (*Dendroica discolor*)	FBMR	C	76	16	21.0	Howell (1998)
	PNWR	C	107	9	8.4	Brunjes (1998), Raftovitch (1998)
	SRS	U	8	1	12.5	CEM (unpubl.)
Total			191	26	13.6	
Swainson's Warbler (*Limnothlypis swainsonii*)	SRS	R	6	0	0	Moorman (1999), R. A. Sargent et al. (unpubl.)
Ovenbird (*Seiurus aurocapillus*)	SRS	R	11	0	0	P. J. Champlin and JCK (unpubl.)
Kentucky Warbler (*Oporornis formosus*)	SRS	U	33	0	0	Sargent et al. (1997), Moorman (1999)
Common Yellowthroat (*Geothlypis trichas*)	SRS	C	7	0	0	Moorman (1999), R. A. Sargent et al. (unpubl.)
Hooded Warbler (*Wilsonia citrina*)	SRS	U	132	19	14.4	Sargent et al. (1997), Moorman et al. (2002)
Yellow-breasted Chat (*Icteria virens*)	FBMR	V	46	8	17.4	Howell (1998)
	PNWR	V	30	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	C	2	0	0	CEM (unpubl.)
	JISC	V	35	13	37.1	Whitehead et al. (2000)
Total			113	21	18.6	
Summer Tanager (*Piranga rubra*)	PNWR	C	16	1	6.3	Brunjes (1998), Raftovitch (1998)

TABLE 2. Continued.

Species	Site	Relative abundance[a]	Number of nests	Number parasitized	Percent	Source
Northern Cardinal (*Cardinalis cardinalis*)	FBMR	A	31	1	3.2	Howell (1998)
	PNWR	A	49	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	A	59	0	0	Moorman (1999), R. A. Sargent et al. (unpubl.)
	JISC	A	92	5	5.4	Whitehead et al. (2000)
Total			231	6	2.6	
Indigo Bunting (*Passerina cyanea*)	FBMR	V	54	12	22.2	Howell (1998)
	PNWR	V	22	3	13.6	Brunjes (1998), Raftovitch (1998)
	SRS	V	11	0	0	Moorman (1999, unpubl.), R. A. Sargent et al. (unpubl.)
	JISC	V	22	3	13.6	Whitehead et al. (2000)
Total			109	18	16.5	
Painted Bunting (*Passerina ciris*)	JISC	C	17	6	35.3	Whitehead et al. (2000)
Blue Grosbeak (*Guiraca caerulea*)	PNWR	C	5	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	V	5	0	0	CEM (unpubl.), R. A. Sargent et al. (unpubl.)
	JISC	C	22	6	27.3	Whitehead et al. (2000)
Total			32	6	18.8	
Eastern Towhee (*Pipilo erythrophthalmus*)	FBMR	V	44	1	2.2	Howell (1998)
	PNWR	V	53	1	1.9	Brunjes (1998), Raftovitch (1998)
	SRS	V	12	2	16.7	Krementz and Powell (2000), CEM (unpubl.)
Total			109	4	3.7	
Red-winged Blackbird (*Agelaius phoeniceus*)	JISC	V	73	2	2.7	Whitehead et al. (2000)
Orchard Oriole (*Icterus spurious*)	PNWR	U	1	0	0	Brunjes (1998), Raftovitch (1998)
Bachman's Sparrow (*Aimophila aestivalis*)	FBMR	R	13	0	0	Howell (1998)
	PNWR	R	2	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	U	41	0	0	Stober and Krementz (2000)
Total			56	0	0	
Field Sparrow (*Spizella pusilla*)	PNWR	C	9	0	0	Brunjes (1998), Raftovitch (1998)
	SRS	C	1	0	0	CEM (unpubl.)
Total			10	0	0	
Total (all species)			1,372	113	8.2	
Total (parasitized species)			1,212	113	9.3	

[a] Relative abundance indexed by number of detections per Breeding Bird Survey route: R = rare (≤1); U = uncommon (2–3); C = common (4–10); V = very common (11–30); A = abundant (31–100); from distribution maps provided by Sauer et al. (2003).

nesting species were not. Of 105 ground nests from four species (Ovenbird, *Seiurus aurocapillus*; Kentucky Warbler; Common Yellowthroat, *Geothlypis trichas*; and Bachman's Sparrow, *Aimophila aestivalis*), none were parasitized. Although cowbirds parasitize these species preferentially in other portions of their range (Hahn and Hatfield 2000), ap-

parently ground-nesting birds are not important cowbird hosts in the southern Atlantic Coastal Plain and Piedmont.

Even among the frequent hosts, overall parasitism rates were low relative to those reported from other regions. Painted Buntings suffered the highest parasitism rate (35.3%), but this rate was based on a moderate sample size, and all nests were from the same site (James Island). Among the remaining frequent host species, overall parasitism rates were <20%, ranging from 11–19%. In contrast, Hooded Warblers have been reported to experience 45%, 62%, and 75% parasitism in Ontario, Pennsylvania, and Illinois, respectively (Evans Ogden and Stutchbury 1994). Similarly, White-eyed Vireos reportedly experienced 40% (6 of 15), 48% (23 of 47), and 83% (10 of 12) parasitism in Louisiana (Goertz 1977), Virginia (Hopp et al. 1995), and Illinois (Graber et al. 1985), respectively.

The impact of brood parasitism on the seasonal fecundity of hosts at the levels reported here apparently is minimal. Although parasitism reduced the clutch size of Painted Buntings by approximately one egg, Whitehead et al. (2000) concluded that it did not affect the seasonal fecundity of the species, based on application of the seasonal fecundity model of Pease and Grzybowski (1995). Similarly, Moorman et al. (2002) concluded that the effect of parasitism on Hooded Warbler nesting success was minimal. Whitehead et al. (2000) felt that in their study, low parasitism intensity (i.e., number of cowbird eggs per nest), double brooding by most hosts, and the ability of the hosts to raise cowbird young with their own, ameliorated the impacts of brood parasitism on seasonal fecundity. Of the studies summarized here, only Whitehead et al. (2000) reported the extent of double brooding. All six species they examined attempted two broods per year, except Yellow-breasted Chats. In several of the reported studies low parasitism intensity was observed; the number of cowbird eggs per parasitized nest was only slightly greater than one (1.0, Raftovitch 1998; 1.0, R. A. Sargent et al. unpubl. data; 1.1, CEM unpubl. data; 1.2, Sargent et al. 1997). Likewise, two of the reported studies mentioned that most nests that fledged cowbird young also fledged host young (Howell 1998, Moorman et al. 2002). This evidence, coupled with parasitism rates below 35% (i.e., that of Painted Buntings), suggests that the conclusions of Whitehead et al. (2000) regarding the lack of an impact of parasitism on seasonal fecundity may be true for most host populations in the southern Atlantic Coastal Plain and Piedmont.

Wiedenfeld (2000) suggested that it is probably not necessary to focus cowbird research in the southeastern Coastal Plain, though he believed monitoring of cowbird population levels was warranted. We agree that brood parasitism does not appear to present an immediate threat to the stability of most host populations in the region. However, we suggest that further research is needed on certain aspects of cowbird parasitism in the Southeast. For example, impacts on the seasonal fecundity of single-brooded species in the region (e.g., Yellow-breasted Chats) are poorly understood. Also, further study is warranted on species whose southeastern populations are considered sensitive, such as Painted Buntings, Swainson's Warblers (*Limnothlypis swainsonii*), and Black-throated Green Warblers (*Dendroica virens*; Hunter et al. 2001). Finally, additional information is needed from southeastern landscapes fragmented and dominated by suburban and agricultural habitat, where cowbird abundance may be greater than in the study areas reported here. Parasitism rates at James Island were slightly higher than at the other sites. James Island was converted from a forest and agricultural landscape to a developed landscape since the mid-1980s. As other portions of the Southeast undergo a similar process, the effect of such transition on cowbird parasitism dynamics warrants careful attention.

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NEST SUCCESS AND HABITAT SELECTION OF THE SEMIPALMATED PLOVER ON AKIMISKI ISLAND, NUNAVUT

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ABSTRACT.—We studied nest site selection by Semipalmated Plovers (*Charadrius semipalmatus*) to compare microhabitat characteristics at nest and random sites, and to compare successful and unsuccessful nests on the northern shore of Akimiski Island, Nunavut, during 2002. Nesting birds selected sites with more pebbles and less vegetative cover than randomly available in the environment. Nest sites also had smaller percentage of bare mud than random sites. Plovers selected sites within 100 m of Arctic Terns (*Sterna paradisaea*) more often than expected based on the distribution of random sites in the study area. Twenty-three of 41 (56%) nests hatched successfully. None of the microhabitat features that we measured predicted nest success. All 10 nests near the colony of Arctic Terns hatched, suggesting that interspecific associations are more reliable than habitat features for predicting nest success. *Received 10 May 2003, accepted 25 September 2003.*

Nest site selection in shorebirds has important consequences for their survival and reproduction (Dyrcz et al. 1981, Espie et al. 1996, Powell 2001). Although the behavioral mechanisms of selection are poorly understood, the outcome is a nonrandom distribution of nests among available sites (Cody 1985, Lauro and Nol 1995). Nest predation may be the most important selective pressure affecting nest success (Lauro and Nol 1995, Lloyd et al. 2000). If microhabitat differences exist between successful and unsuccessful sites, natural selection may modify adaptive strategies (e.g., which habitats are used for nesting) to reduce predation risk. While other factors such as access to food for adults and/or young (Lauro and Nol 1995) and interspecific interactions (Dyrcz et al. 1981, Burger 1987, Powell 2001), influence nest site selection, predation risk is more important in the immediate vicinity of the nest. This general principle is the basis for numerous studies attempting to associate microhabitat structures with used and available sites, as well as successful and unsuccessful sites (Flemming et al. 1992, Espie et al. 1996, Powell 2001).

The Semipalmated Plover (*Charadrius semipalmatus*) is a common shorebird of open habitats in the Arctic and sub-Arctic regions of North America (Nol and Blanken 1999). There are numerous accounts of the breeding biology of this species (Sullivan Blanken and Nol 1998, Nol and Blanken 1999), but little quantitative information is available on microhabitat characteristics of their nest sites (Nol and Blanken 1999). This species and other members of the genus rely on crypsis to enhance nest success. Some authors have argued that objects near the nest increase crypsis (e.g., Graul 1973, Lloyd et al. 2000). Therefore, we might expect that features around the nest and variation in these features would be related to variation in reproductive success. Hence, we compared physical and vegetation characteristics of Semipalmated Plover nest sites to random sites, and of successful and unsuccessful nests on Akimiski Island, Nunavut, Canada.

METHODS

Study area.—We studied plovers nesting on the northern shore of Akimiski Island, Nunavut, Canada (53° 11′ N, 81° 35′ W) between 4 June and 29 July 2002. The 3,800-km^2 island is located approximately 20 km offshore from the mouth of the Attawapiskat River in western James Bay (Leafloor et al. 2000). Our approximately 14-km^2 study area consisted of intertidal and supratidal salt marshes, including strand beaches and sand-gravel depositional areas surrounded by mudflats. Semipalmated Plovers nested in various densities at these beaches and sand-gravel depositional areas. Vegetation changed along a gradient, and was dominated by creeking alkali grass (*Puccinellia phryganodes*) in the lower intertidal marsh to fescue (*Festuca rubra*), Arctic rush

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(*Juncus arcticus*), Baltic rush (*J. balticus*), and Hoppner's sedge (*Carex subspathacea*) in the upper intertidal marsh and supratidal marsh (Blaney and Kotanen 2001). The transition from supratidal marsh to freshwater areas was characterized by willow (*Salix* spp.) shrubs, interspersed with water sedge (*C. aquatilis*) and buttercup (*Ranunculus* spp.) around pools. Vegetation in the supratidal marsh has been moderately degraded by the foraging of nesting Canada Geese (*Branta canadensis*). A small (<20 pairs in a 17-ha area) Arctic Tern (*Sterna paradisaea*) colony was present within our study area.

Nest searching and monitoring.—We found nests by walking through potential breeding habitat using parental behavior (distraction displays, or crouching) as an indicator of presence of nesting pairs (Nol and Blanken 1999). We monitored nests every 1–4 days until we could determine nest fate. We defined each nest as successful if at least one egg hatched. We considered eggs abandoned if they were cold and/or no adults were in the area on two successive visits. We examined nests for evidence of predation (tracks, broken eggshells, or punctured eggs) or hatching (distraction displays, observation of adults with chicks, or clean eggshell remnants in the nest; Mabee 1997) if nest contents were gone prior to the estimated hatch date. We assumed 5 days for laying and 24 days for incubation (Nol and Blanken 1999).

Nesting habitat.—We documented physical and vegetation characteristics within a 1-m^2 quadrat centered on the nest using a Canon Powershot S40 digital camera (Canon Canada Inc., Mississauga, Ontario) at approximately 1.5 m above the nest (Flemming et al. 1992). We determined random sites within our study area by selecting numbers from a random numbers table and plotting the values in an X-Y coordinate system using ArcView (Environmental Systems Research Inst. 1999). We located these random sites using a Global Positioning System (GARMIN International Inc., Olathe, Kansas), and we eliminated from our sample those sites that were not located on potential nest substrates (e.g., a site on water).

For analyses of the image of each quadrat, we superimposed a grid of 400 5 × 5 cm cells using Paint Shop Pro (Jasc Software 2000). We estimated percent cover of pebbles (<5 cm diameter), stones (5–10 cm), rocks (>10 cm), mollusc shells, sticks (>10 cm length), and bare mud (i.e., having neither vegetation nor pebbles) based on occurrence in these cells (Flemming et al. 1992). In situations where two or more substrate or vegetation characteristics occurred in each cell, we classified the cell by the dominant characteristic.

We estimated percent cover of low (<5 cm vegetation height) and tall vegetation (>5 cm) at the nest site, as well as vegetation height, using the mean of the values obtained at the four corners of the quadrat. We measured distances from the nest to the nearest 1-m^2 patch of vegetation, open water (coast of James Bay or small supratidal ponds), shrub or tree (area with >1 m vegetation height), and vertical obstruction (area with >10 cm diameter) using a 60-m tape, and/or pacing. We measured distances to the nearest shrub or tree, up to a maximum distance of 500 m. We estimated maximum length and width of the habitat patch (i.e., an area differing from its surroundings) that contained the nest site by measuring where the habitat changed (e.g., gravel to bare mud). We determined elevation by pulling a string placed at the nest cup to a permanent source of surface water, held the string horizontal, and measured the vertical distance between string and water. We determined slope by placing one end of a straight object of known length at the nest cup. The other end was touching the substrate. We raised this end until the object was parallel to the ground. We estimated slope with the TAN-1 function from the vertical distance of the object held level above the substrate, and length of the object. We estimated height of vertical obstruction at the four corners of the 1-m^2 quadrat with a tape measure. We estimated percent cover of vertical obstruction with the mean of the values obtained at the four corners of the quadrat using a transparent 20 × 20 cm checkerboard (100 2 × 2 cm cells) held vertically at the nest site.

Statistical analyses.—We eliminated from all analyses two habitat variables (percent cover of tall vegetation and sticks) that were absent from more than 25% of the nest and random sites. Sixteen variables were used to describe the structure of the microhabitat at nest and random sites (Table 1). We per-

TABLE 1. Eigenvectors, eigenvalues, and variances explained for principal components analysis of habitat variables measured at 42 Semipalmated Plover nest and 84 random sites on Akimiski Island, Nunavut, Canada, 2002. Correlation loadings >|0.40| are in boldface.

Habitat variables	Eigenvectors		
	PC1	PC2	PC3
Vegetation height	−0.36	−0.30	−0.15
Distance to 1-m² vegetation	0.24	0.09	0.20
Distance to open water	0.15	0.03	−0.20
Distance to shrub or tree	0.27	0.15	−0.19
Distance to vertical obstruction	−0.05	0.30	−0.05
Length of habitat patch	0.28	0.07	−0.18
Width of habitat patch	0.39	−0.01	−0.26
Elevation	0.26	−0.29	−0.30
Slope	−0.11	−0.13	−0.14
Percent cover of vertical obstruction	−0.16	**−0.41**	−0.13
Percent cover of pebbles	**0.40**	−0.33	0.15
Percent cover of stones	0.00	−0.23	**0.42**
Percent cover of rocks	0.12	−0.29	**0.42**
Percent cover of mollusc shells	0.18	−0.05	−0.38
Percent cover of low vegetation	**−0.43**	−0.06	−0.31
Percent cover of bare mud	−0.07	**0.52**	0.13
Eigenvalue	2.94	2.62	1.76
Percent total variance	18.40	16.40	11.00

formed principal components analysis (PCA) using MINITAB 13.1 (MINITAB Statistical Software 2000) to summarize the patterns of covariation present in those variables. We retained six components based on eigenvalues >1.0, but we report only the three components which each explained >10% of the variance. We standardized all measurements. We compared the means of the six principal components for nest and random sites using independent *t*-tests, but report only statistically significant components. We considered a test to be statistically significant at the 5% level if $P \leq 0.008$ after we applied Bonferroni's correction to these data.

We performed logistic regression using SPSS 9.0 (SPSS, Inc. 1998) to model which microhabitat variables should be included in the final model with nest success as the binary response variable (Manly 1994). We constructed 91 potential models via a manual forward selection method, where we made univariate and multivariate comparisons of habitat variables between successful and unsuccessful nests.

We further excluded five variables (vegetation height, percent cover of stones, percent cover of mollusc shell, percent cover of low vegetation, and percent cover of bare mud) because they were absent at >25% of the nest sites. This approach resulted in eleven variables, which we transformed before analyses to improve the normality of their distributions. We arbitrarily divided distance to shrub or tree into one of six categories: <99 m, 100–199 m, 200–299 m, 300–399 m, 400–499 m, and >500 m. We determined correlation coefficients for pairs of habitat descriptors, and we retained those variables with $r < 0.6$. We eliminated the least significant correlated variables based upon partial correlations for distance to open water, length of substrate, and width of substrate. We retained the variable with the lowest standard error of the estimate for distance to 1-m² patch of vegetation and percent cover of pebbles. We used the variables: distance to open water, distance to vertical obstruction, distance to shrub or tree, elevation, slope, percent cover of vertical obstruction, percent cover of pebbles, and percent cover of rocks in our model. Unless otherwise stated, we set statistical significance at $\alpha = 0.05$.

RESULTS

Comparison of nest and random sites.—The PCA of 16 habitat variables measured at 42

TABLE 2. Means of the principal components, including the variables that loaded onto each component, were significantly different between Semipalmated Plover nest and random sites on Akimiski Island, Nunavut, Canada, 2002. Nest sites had more pebbles in the substrate and less vegetative cover (PC1), and greater vertical obstruction and less bare mud (PC2) than random sites.

Component	Nest		Random				
	Mean	SE	Mean	SE	*t*	df	*P*
PC1	0.7	0.3	−0.4	0.2	3.52	124	0.001
Percent cover of pebbles	63.6	4.3	30.4	3.9			
Percent cover of low vegetation	17.1	3.6	29.5	3.7			
PC2	−1.1	0.1	0.6	0.2	7.77	123	<0.001
Percent cover of obstruction	21.0	1.5	16.5	1.7			
Percent cover of bare mud	5.2	1.8	35.6	3.9			

nest and 84 random sites extracted six components that accounted for 67% of the total variance in the sample. PC1 represented a gradient from sites with large proportions of vegetative cover (negative values) to large proportions of pebble substrate (positive values; Table 1). Nest sites had significantly greater values of PC1 than random sites, indicating more pebbles in the substrate and less vegetative cover (Table 2). PC2 represented a gradient of visibility with negative values indicating more vertical obstruction while positive values indicated a greater percentage of bare mud. Nest sites had less mud than random sites (Table 2). PC2, PC3, and PC4 did not differ significantly between nest and random sites (powers < 0.30). The proportion of nest sites that were <100 m from the Arctic Tern colony (10 of 42, 24%) was significantly greater than proportion of random sites <100 m to the colony (5 of 84, 6%; Fisher's exact test, $P = 0.005$).

Probability of nest success.—Nest fate was known for all nests (18 unsuccessful and 23 successful) but one. Although multiple logistic regression showed no significant relationship between nest success and habitat variables ($\chi^2 = 8.38$, df = 8, $P = 0.40$), distance to vertical obstruction contributed significantly to the model when this habitat feature was entered individually (Wald's $\chi^2 = 4.04$, df = 1, $P = 0.044$; Table 3). In the univariate analysis, distance to vertical obstructions was not significantly different between successful and unsuccessful nests (means of 0.45 m ± 0.20 SE and 0.19 m ± 0.08 SE; respectively; $\chi^2 = 2.93$, df = 1, $P = 0.083$), although power for this test was low (0.40). The final multivariate model retained distance to the nearest vertical obstruction and slope ($\chi^2 = 5.45$, df = 2, $P = 0.065$). The proportion of successful nests <100 m from the Arctic Tern colony (10 of 10, 100%) was significantly greater than the proportion of successful nests found farther from the colony (13 of 31, 42%; Fisher's exact test, $P = 0.026$). Habitat characteristics be-

TABLE 3. Multiple logistic regression of the relationship between Semipalmated Plover nest success and individual habitat variables on Akimiski Island, Nunavut, Canada, 2002.

Habitat variable	Successful		Unsuccessful			
	Mean	SE	Mean	SE	Wald's χ^2	*P*
Distance to open water (m)	6.0	1.4	5.4	1.5	0.03	0.85
Distance to shrub or tree (m)	4.3	0.4	4.1	0.5	0.01	0.91
Distance to vertical obstruction[1] (m)	0.5	0.2	0.2	0.1	4.04	0.04
Elevation (cm)	22.1	1.2	21.9	1.3	0.41	0.50
Slope (°)	1.6	0.1	2.5	0.2	3.00	0.08
Percent cover of vertical obstruction	19.1	1.1	18.7	1.1	0.63	0.43
Percent cover of pebbles	60.0	6.7	67.1	5.2	0.42	0.52
Percent cover of rocks	1.9	0.2	2.5	0.3	0.46	0.50

[1] Logistic regression ($\chi^2 = 2.93$, $P = 0.083$, power = 0.40) showed no difference between successful and unsuccessful nests.

tween successful nests near to and far from the tern colony were not significantly different ($P > 0.14$).

DISCUSSION

Semipalmated Plovers placed their nests nonrandomly with respect to substrate and vegetation characteristics, but these microhabitat characteristics were not associated with nest success. Most nest sites contained >10% pebble substrate, and this was significantly greater than the proportion available in the surrounding environment. Similarly, other members of this genus (Piping Plovers, *C. melodus*: Burger 1987, Flemming et al. 1992; Killdeer, *C. vociferus*: Nol and Lambert 1984; Snowy Plovers, *C. alexandrinus*: Powell 2001; Mountain Plovers, *C. montanus*: Olson and Edge 1985) selected nest sites in microhabitats with a larger pebble component than that randomly available in the environment. Pebbles may help camouflage the eggs and chicks against the surrounding environment to reduce the risk of predation (Flemming et al. 1992). Gotmark et al. (1995) reported two types of nest concealment: concealment by vegetation and concealment by cryptic coloration of incubating birds and their eggs. Although vegetative cover may provide disruptive camouflage or concealment of incubating birds (Lloyd et al. 2000), we suggest that concealment by cryptic plumage may be more important than concealment by vegetation in plovers. Plovers selected nest sites with lower vegetative cover than that randomly available in the surrounding environment, suggesting a threshold where visibility is more advantageous than concealment by vegetation (Gotmark et al. 1995). Nest predation may have been the strong selective force operating on site selection by Semipalmated Plovers because the variables (i.e., pebble substrate with sparse vegetation) selected could reflect antipredator strategies (Graul 1973). Alternatively, nest sites in pebble substrates may provide a surface for retaining heat because eggs placed on pebbles may cool down at a slower rate than eggs placed on bare mud (Reid et al. 2002).

Vertical obstructions in this area generally were low (<20% of cells in our grid were covered), and similar to the general surrounding microhabitat. Habitats were mostly open as found for virtually all other beach or supratidal nesting shorebirds (Nol and Lambert 1984, Olson and Edge 1985, Lauro and Nol 1995). Nesting in relatively open habitat may provide good visibility to facilitate: (1) detection of a nest predator from the nest, (2) conspecific communication, and/or (3) detection of prey or foraging conspecifics (Gotmark et al. 1995). Early detection of nest predators is important for defense in plovers because they rely on crypsis (Graul 1973) and distraction displays to prevent nest predation (Nol and Blanken 1999). Territory defense against foraging conspecifics also may be facilitated if nests were not fully hidden.

The main component of PC2 that varied between nest and random sites was the small proportion (<6%) of bare mud in the nest quadrat, suggesting that plovers may be avoiding sites with a large proportion of muddy substrate. Nests placed in bare mud remain exposed, whereas nests placed in pebble substrates may be concealed because of the cryptic pigmentation of plover eggs. This may be relevant because sympatric Arctic geese (Canada Geese, *B. canadensis*, and Snow Geese, *Chen caerulescens caerulescens*) have overgrazed soil-binding vegetation on western parts of Akimiski Island, resulting in a transition from sub-Arctic coastal salt marsh to extensive denuded areas (Srivastava and Jefferies 1996). This may reduce the sand-gravel depositional areas preferred by plovers through tidal flooding. The degree to which Arctic geese impact nest site availability of shorebirds throughout the eastern Arctic deserves further study.

Selection of nonrandom sites for nest placement suggests long term natural selection on choice of nest sites. Although our results showed that none of the habitat variables were strong predictors of nest success, diverse predators occur in our study. Potential predators of either eggs or young included the American Crow (*Corvus brachyrhyncos*), Common Raven (*C. corax*), Herring Gull (*Larus argentatus*), Peregrine Falcon (*Falco peregrinus*), red fox (*Vulpes vulpes*), shorttail weasel (*Mustela erminea*), and striped skunk (*Mephitis mephitis*). Nest searching techniques, and the ability to detect nest site patches, vary substantially among these predators so that no single set of habitat characteristics may offer complete pro-

tection (Chase 2002). Clear associations between nest site characteristics and nest success are difficult to demonstrate without experimental manipulations (Colwell and Oring 1990, Chase 2002). Semipalmated Plovers appear to benefit substantially from the protection against predators afforded by the aggressive nest defense behavior of Arctic Terns on Akimiski Island. Thus, this species may be added to the list of shorebirds that, at least sometimes, choose to nest in colonial bird colonies to exploit this advantage (Dyrcz et al. 1981, Burger 1987, Powell 2001). The degree to which plovers alter their timing of breeding to coincide with that of nesting terns currently is under study.

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RESPONSES OF BIRD COMMUNITIES TO EARLY SUCCESSIONAL HABITAT IN A MANAGED LANDSCAPE

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ABSTRACT.—I examined short and long term responses of breeding bird communities to the systematic creation of early successional habitat resulting from forest management at a 1,120-ha study site in the Ridge and Valley Province of Pennsylvania, from 1998 through 2002. Species richness and abundances of all species combined and of early successional species increased from precut (1998–1999) to postcut eras (2001–2002) in a treated sector (aspen, *Populus* spp., and mixed oak, *Quercus* spp., areas combined), an uncut control sector, and the total study site (treated and control sectors combined) after the fourth cutting cycle. Abundances of a woodland species (Red-eyed Vireo, *Vireo olivaceus*) and four early successional species (e.g., Field Sparrow, *Spizella pusilla*) also increased. Over the past 15 years, which spans the third and the fourth cutting cycles at the study site, three woodland species increased significantly in both treated and control sectors (Red-eyed Vireo) or in the treated sector only (Ovenbird, *Seiurus aurocapillus*, and American Redstart, *Setophaga ruticilla*). The population of an early successional species (Indigo Bunting, *Passerina cyanea*) increased significantly in both treated and control sectors. Population trends of three woodland and three early successional species at the study site paralleled statewide or provincial increases in these species over the past two decades. My study has shown that the management of early successional habitats in extensively forested areas will be of benefit for the long term conservation of both early successional and mature forest bird species within a forested landscape. *Received 10 February 2003, accepted 29 June 2003.*

Long term studies focusing on wildlife responses to forest management are relatively scarce, yet are crucial to an understanding of regional trends in populations (Gullion 1990, Yahner 2000). In the northeastern United States, forest maturation and farm abandonment likely are responsible for population declines of a variety of wildlife dependent upon early successional habitat (Litviatis 1993, Brawn et al. 2001, Trani et al. 2001). Thus, an important question is whether habitat can be created for conservation of both early successional and mature forest species within the same managed forested landscape.

The Barrens Grouse Habitat Management Area (GHMA) was established in 1976 for the systematic creation of habitat for Ruffed Grouse (*Bonasus umbellus*) through even-aged management (Yahner 1993). This was achieved by establishment of 4-ha "activity centers" for adult grouse (Gullion 1977), giving an interspersion of 1-ha contiguous plots of different ages in aspen (*Populus* spp.) and mixed oak (*Quercus* spp.) cover types (Yahner 1993, 1997). Grouse habitat management at the Barrens GHMA has the potential to provide valuable breeding habitat for coexisting bird species dependent upon young forested plots. My objectives were to (1) compare bird community structure and composition immediately before and after a fourth cutting cycle at the Barrens GHMA and (2) examine trends in populations of individual species (in particular, early successional species dependent upon stands <3 years since cutting) in response to creation of additional early successional habitat resulting from the fourth cutting cycle. I compared these results to those obtained at the Barrens GHMA immediately after the third cutting cycle (Yahner 1993) and to those obtained 5–8 years after the third cutting cycle (Yahner 1997).

METHODS

I conducted my study at the 1,120-ha Barrens Grouse Habitat Management Area (GHMA; 40° 47′ N, 78° 58′ W) on State Game Lands 176, Centre County, in the Ridge and Valley Province of Pennsylvania (Yahner 1993, 1997). The Barrens GHMA was divided into an uncut control sector and a treated sector of approximately equal size (576 ha and 544 ha, respectively).

The treated sector consisted of 136 contiguous 4-ha blocks; each block was subdivided into 1-ha plots (A–D, each 100 × 100 m) arranged in a clockwise fashion (Yahner 1993, 1997, 2000). Plots A–D in 60 blocks (240 ha,

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aspen area) were cut systematically during four cutting cycles (winters 1976–1977, 1980–1981, 1986–1987, and 1999–2000), whereas plots A–C in 76 blocks (304 ha, mixed oak area) were cut during three cutting cycles (winters 1976–1977, 1986–1987, 1999–2000). Subsequent to the initial three cutting cycles, 75% of the plots in the aspen area and 50% of the plots in the mixed oak area were cut; but after the fourth cutting cycle (1999–2000), all plots in the aspen area were cut and 75% of the plots in the mixed oak area were cut. In plots cut during the third and fourth cutting cycles (plots C and D in the aspen area, plots B and C in the mixed oak area), 15–20 overstory trees per plot were retained.

Major overstory trees (woody stem >7.5 cm dbh, >1.5-m tall) in uncut habitat (control sector and plot D in the mixed oak area) were white oak (*Quercus alba*), chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), red maple (*Acer rubrum*), bigtooth aspen (*Populus grandidenta*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*; Yahner 1993, 1997). Overstory trees were about 80–90 years old. Principal understory woody species included oak, red maple, aspen, and black cherry (*Prunus serotina*).

I selected 90 representative 1-ha plots for bird sampling, with 10 plots in the control sector and 80 plots in aspen and mixed oak areas (10 each of plots A–D per area). These were the same 90 plots used during previous studies at the Barrens GHMA (plot selection and avian sampling protocols follow Yahner 1993, 1997). Plots selected were separated by >200 m, and centers of plots were >50 m from disturbances (e.g., logging roads) to reduce edge effects (Strelke and Dickson 1980, Yahner 1987).

I visited each plot once per year in late May to early June in 1998 and 1999 immediately prior to the fourth cutting cycle (precut era) and in late May to early June in 2001 and 2002 (postcut era). The randomized order of visits and number of visits per plot were identical to those of previous studies (Yahner 1993, 1997). After a 1-min equilibrium period, I counted all birds seen or heard within 30 m of each plot center, using a 5-min point count; counts were made between sunrise and 09:00 EST. A 30-m radius positioned in the plot center minimized edge effects at the interfaces between plots of different age in the treated sector (Repenning and Labisky 1985). Birds flying over a plot were not counted, and movements of individual birds were monitored carefully to minimize counting the same bird twice.

I calculated species richness and total abundance for each of the three areas (aspen area, mixed oak area, and control sector) during precut and postcut eras (after Yahner 1993, 1997). Species richness was the total number of species, and total abundance was the number of contacts/100 ha of all species combined. In addition, I calculated abundances of individual species for each area during both eras.

To compare short term responses of bird populations at Barrens GHMA to creation of additional early successional habitat, I compared observed to expected numbers of contacts for all species combined, for early successional species combined, and for individual species with adequate sample sizes (>10 contacts combined) between eras in each area separately and for the total study site with χ^2 goodness-of-fit tests (Sokal and Rohlf 1995). I calculated expected number of contacts per era as the total number of contacts observed in both eras combined divided by 2.

I also contrasted observed and expected numbers of contacts of individual bird species between precut and postcut eras in plots cut during the fourth cycle (plot D in the aspen area and plot C in mixed oak area) using χ^2 goodness-of-fit tests; expected numbers of contacts were calculated as the total number observed in these two plot types during both eras combined divided by 2.

To compare long term trends in bird populations at the Barrens GHMA, I examined abundances of individual species immediately subsequent to the third cutting cycle during three breeding seasons (1987–1989; Yahner 1993), during three breeding seasons approximately midway between third and fourth cutting cycle (1993–1995; Yahner 1997), and during two breeding seasons immediately after the fourth cutting cycle (2001–2002; present study). I compared observed to expected numbers of contacts for species with adequate sample sizes (>15 contacts/area) among the

TABLE 1. The abundance (contacts/100 ha) of species varied among areas and between precut and postcut eras at the Barrens Grouse Habitat Management Area, Pennsylvania. In the precut era, 75% of the aspen area and 50% of the mixed oak area were cut in 1998–1999. Actual numbers of contacts are in parentheses. Only common (≥10 contacts) species are shown, but contacts of uncommon species are included in values of species richness and total abundance.[a]

	Precut era (1998–1999)			
	Aspen	Mixed oak	Control	Total site
Ruffed Grouse, *Bonasa umbellus*	4 (1)	13 (3)	18 (1)	10 (5)
Great Crested Flycatcher, *Myiarchus crinitus*	4 (1)	13 (3)	35 (2)	12 (6)
Eastern Wood-Pewee, *Contopus virens*	0 (0)	13 (3)	53 (3)	12 (6)
Blue Jay, *Cyanocitta cristata*	22 (5)	18 (4)	18 (1)	20 (10)
Tufted Titmouse, *Baeolophus bicolor*	4 (1)	31 (7)	0 (0)	16 (8)
Black-capped Chickadee, *Poecile atricapillus*	31 (7)	4 (1)	0 (0)	16 (8)
Blue-gray Gnatcatcher, *Polioptila caerulea*	0 (0)	9 (2)	0 (0)	4 (2)
Wood Thrush, *Hylocichla mustelina*	4 (1)	13 (3)	0 (0)	8 (4)
Gray Catbird, *Dumetella carolinensis*	70 (16)	31 (7)	0 (0)	46 (23)
Cedar Waxwing, *Bombycilla cedrorum*	0 (0)	13 (3)	35 (2)	10 (5)
Red-eyed Vireo, *Vireo olivaceus*	62 (14)[c]	92 (23)	248 (14)	102 (51)[c]
Golden-winged Warbler, *Vermivora chrysoptera*[b]	9 (2)	0 (0)	0 (0)	4 (2)
Black-and-white Warbler, *Mniotilta varia*	35 (8)	13 (3)	0 (0)	22 (11)
Chestnut-sided Warbler, *Dendroica pensylvanica*[b]	22 (5)	22 (5)	0 (0)	20 (10)
Ovenbird, *Seiurus aurocapillus*	207 (47)	70 (16)	142 (8)	142 (71)
Common Yellowthroat, *Geothlypis trichas*[b]	31 (7)	35 (8)	0 (0)	30 (15)[c]
American Redstart, *Setophaga ruticilla*	35 (4)	106 (24)	106 (6)	68 (34)
Rose-breasted Grosbeak, *Pheucticus ludovicianus*	22 (5)	26 (6)	0 (0)	22 (11)
Northern Cardinal, *Cardinalis cardinalis*	0 (0)	4 (1)	0 (0)	2 (1)
Indigo Bunting, *Passerina cyanea*[b]	0 (0)	0 (0)	0 (0)	0 (0)[c]
Eastern Towhee, *Pipilo erythrophthalmus*[b]	92 (21)	35 (8)	0 (0)	58 (29)
Field Sparrow, *Spizella pusilla*[b]	4 (1)[c]	0 (0)	0 (0)	2 (1)[c]
Chipping Sparrow, *Spizella passerina*[b]	4 (1)	4 (1)	0 (0)	4 (2)
Brown-headed Cowbird, *Molothrus ater*	4 (1)	22 (5)	17 (1)	14 (7)
Scarlet Tanager, *Piranga olivacea*	18 (4)	31 (7)	106 (6)	34 (17)
Species richness, all species combined	25	31	14	34
Species richness, early successional species	7	4	0	6
Total abundance, all species combined	695 (158)[c]	559 (127)[c]	832 (48)	726 (363)[c]
Total abundance, early successional species	163 (37)[c]	97 (22)[c]	0 (0)	118 (59)[c]

[a] Including Northern Flicker (*Colaptes auratus*; two in aspen area and one in mixed oak area) and Yellow-breasted Chat (*Icteria virens*; one in aspen area); both species in postcut era.
[b] Early successional species adapted to young (≤3 years since cutting) forested plots.
[c] Observed and expected number of contacts differed significantly between eras (see text for *P* values).

three time periods in treated and control sectors separately using χ^2 goodness-of-fit tests. I calculated expected numbers of contacts as the total number of contacts observed in all three time periods combined for a given sector divided by 3 or 2 (depending upon the period length). If abundances were significantly different among time periods in a given sector, I used *a posteriori* χ^2 goodness-of-fit tests about the time period of interest.

RESULTS

Species richness of all species and of early successional species increased from precut to postcut eras throughout the Barrens GHMA (Table 1). Furthermore, abundances of all species combined and of early successional species increased significantly between eras in the aspen area (both $P < 0.0001$), the mixed oak area ($P = 0.0005$ and $P = 0.003$, respectively), and the total site (both $P < 0.0001$). Abundance of a woodland species, the Red-eyed Vireo (*Vireo olivaceus*), also increased significantly between eras in the aspen area ($P = 0.012$) and total site ($P = 0.005$). Similarly, abundances of four early successional species increased from precut to postcut eras in the total site (Common Yellowthroat, *Geothlypis trichas*, $P = 0.037$; Indigo Bunting, *Passerina cyanea*, $P < 0.0001$; Field Sparrow, *Spizella*

TABLE 1. EXTENDED.

Postcut era (2001–2002)			
Aspen	Mixed oak	Control	Total site
18 (4)	4 (1)	36 (2)	14 (7)
9 (2)	18 (4)	53 (3)	18 (9)
0 (0)	22 (5)	36 (2)	14 (7)
13 (3)	26 (6)	71 (4)	26 (13)
0 (0)	4 (1)	71 (4)	10 (5)
26 (6)	13 (3)	18 (1)	20 (10)
9 (2)	18 (4)	53 (3)	18 (9)
18 (4)	26 (6)	0 (0)	20 (10)
40 (9)	40 (9)	0 (0)	36 (18)
22 (5)	0 (0)	0 (0)	10 (5)
136 (31)	141 (32)	342 (19)	164 (82)
13 (3)	0 (0)	0 (0)	6 (3)
31 (7)	0 (0)	0 (0)	14 (7)
44 (10)	26 (6)	0 (0)	32 (16)
180 (41)	79 (18)	54 (3)	124 (62)
62 (14)	66 (15)	0 (0)	58 (29)
35 (8)	92 (21)	71 (4)	66 (33)
35 (8)	35 (8)	18 (1)	34 (17)
22 (5)	9 (2)	18 (1)	16 (8)
53 (12)	35 (8)	0 (0)	40 (20)
114 (26)	48 (11)	18 (1)	76 (38)
53 (12)	13 (3)	0 (0)	30 (15)
31 (7)	13 (3)	0 (0)	20 (10)
9 (2)	9 (2)	54 (3)	14 (7)
18 (4)	35 (8)	54 (3)	30 (15)
33	30	18	40
9	7	1	9
1,056 (240)	823 (187)	1,062 (60)	974 (487)
383 (87)	207 (47)	18 (1)	270 (135)

pusilla, $P = 0.0006$; and Chipping Sparrow, *Spizella passerina*, $P = 0.020$).

I observed significant declines in use of cut plots in both aspen and mixed oak areas (plots D and C, respectively) of the Barrens GHMA by three woodland species (Red-eyed Vireo, $P = 0.018$; American Redstart, *Setophaga ruticilla*, $P = 0.020$; and Ovenbird, *Seiurus aurocapillus*, $P = 0.043$) immediately after the fourth cutting cycle (Table 2). In contrast, after conversion of these uncut plots to early successional plots, I noted significant and immediate increases in use of these plots by three early successional species (Indigo Bunting, $P < 0.0001$; Eastern Towhee, *Pipilo erythrophthalmus*, $P = 0.004$; and Field Sparrow, $P < 0.0001$).

Over the past 15 years, which spans the third and the fourth cutting cycles at the Barrens GHMA, three woodland species increased significantly in both treated and control sectors (Red-eyed Vireo, $P < 0.0001$ and $P = 0.001$, respectively) or in the treated area only (Ovenbird, $P < 0.0001$; American Redstart, $P < 0.0001$; Table 3). I noted that one early successional species, the Indigo Bunting, increased significantly in the treated sector ($P = 0.015$). The Baltimore Oriole (*Icterus galbula*) was the only species that declined significantly in the treated sector over this time period ($P = 0.028$).

DISCUSSION

My study has shown that species richness and abundances of all species combined and of early successional species increased from

TABLE 2. Some species increased while others decreased between the precut (1998–1999) and postcut (2001–2002) eras in uncut aspen D and oak C plots (see text) combined in the Barrens Grouse Habitat Management Area, Pennsylvania. Only species with ≥5 observations in these plots in both eras combined are shown.

	Contacts		Change (%)
	Precut	Postcut	
Red-eyed Vireo[a]	43	8	−35
Chestnut-sided Warbler	0	56	+56
Ovenbird[a]	35	0	−35
Common Yellowthroat[a]	0	71	+71
American Redstart[a]	36	7	−29
Rose-breasted Grosbeak	18	19	+1
Indigo Bunting[a]	0	100	+100
Eastern Towhee[a]	7	38	+31
Field Sparrow[a]	0	94	+94
Chipping Sparrow	50	67	+17
Scarlet Tanager	73	50	−32

[a] Observed and expected number of contacts differed significantly between precut and postcut eras (see text for *P* values).

precut to postcut eras in part because of greater habitat diversity created by the fourth cutting cycle at the Barrens GHMA. For example, only 30% of the Barrens GHMA was subject to even-aged management immediately after the third cutting cycle (plots of 4 different age classes = 3 different-aged cut plots + uncut plots) compared to 42% of the total area managed in the postcut era (plots of 5 different age classes = 4 different-aged cut plots + uncut plots; Yahner 1997). Moreover, immediately subsequent to the fourth cutting cycle, 12% of the Barrens GHMA was in young, early successional habitat (<3 years since cutting). Thus, a mosaic of forested plots of various ages after the fourth cutting cycle provided suitable habitat for a variety of bird species in a localized area (Yahner 1993, 1997, 2000).

Early successional habitat, such as that created at the Barrens GHMA, has regional and statewide significance to conservation of early successional bird species because forests in Pennsylvania have matured with reduced timber harvest and farm abandonment (Powell and Considine 1982, McWilliams et al. 2002). The significant increase in use of young (<3 years since cutting) forested plots immediately subsequent to the fourth cutting cycle at the Barrens GHMA by Indigo Bunting, Eastern Towhee, and Field Sparrow attests to the value of creating early successional habitats for the benefit of these species (Brawn et al. 2001). Indigo Buntings, in particular, were present in

TABLE 3. Abundance (contacts/100 ha) of some species varied among time periods at the Barrens Grouse Habitat Management Area, Pennsylvania. Only species with ≥15 contacts in a given sector are shown.

	Treated sector			Control sector		
	1987–1989	1993–1995	2001–2002	1987–1989	1993–1995	2001–2002
Blue Jay	21	27	20	0	0	71
Black-capped Chickadee	23	25	20	58	24	18
Wood Thrush	30	18	22	23	0	0
Gray Catbird	81	89	40	0	0	0
Red-eyed Vireo[a]	32[b]	52	139[c]	128[b]	177	336[c]
Golden-winged Warbler	35	35	8	0	0	0
Black-and-white Warbler	16	40	16	12	0	0
Chestnut-sided Warbler	42	56	35	0	0	0
Ovenbird[a]	48[b]	140	131	128	177	54
Common Yellowthroat	128	93	64	0	0	0
American Redstart[a]	0[b]	51	64[c]	0	24	71
Rose-breasted Grosbeak	30	49	35	0	47	18
Indigo Bunting[a]	30	9[b]	44[c]	0	0	0
Eastern Towhee	99	119	81	0	0	18
Field Sparrow	48	30	33	0	0	0
Brown-headed Cowbird	11	30	8	47	59	54
Baltimore Oriole[a]	32[c]	21	0[b]	12	0	0
Scarlet Tanager	27	30	27	71	12	54

[a] Observed and expected number of contacts differed significantly among time periods in a given era (see text for *P* values).
[b] Number of contacts in this time period was significantly lower than in other time periods ($\chi^2 \geq 3.84$, df = 1, $P \leq 0.05$).
[c] Number of contacts in this time period was significantly higher than in other time periods ($\chi^2 \geq 3.84$, df = 1, $P \leq 0.05$).

recently cut plots of the treated sector because of the presence of overstory residual trees, which were used as perch and singing sites, thereby supporting the value of residual trees in cut stands for bird populations (Rodewald and Yahner 2000, Yahner 2000).

I attributed increases in Red-eyed Vireo populations between eras to regional population trends rather than to being a function of forest management at the Barrens GHMA. Based on data obtained from the North American Breeding Bird Survey from 1980–2000, Red-eyed Vireos increased significantly statewide and in the Ridge and Valley Province of Pennsylvania (Sauer et al. 2001). Reduced abundance of Baltimore Oriole populations at the Barrens GHMA paralleled declines in this species noted along Breeding Bird Survey routes in Pennsylvania since the mid-1980s (Robbins et al. 1989).

Two of five early successional species exhibiting population increases from precut to postcut eras (Field Sparrow and Indigo Bunting) at the Barrens GHMA had significant statewide and provincial population declines (Sauer et al. 2001). In addition, populations of a third early successional species (Eastern Towhee) have been reduced significantly in the Ridge and Valley Province. Thus, on a localized basis, the Barrens GHMA provides important breeding habitat to several early successional bird species that are becoming less common on a broader geographic scale (Yahner 1991, 1993, 1997). Similarly, I and others have shown that electric transmission rights-of-way in extensively forested regions of Pennsylvania and elsewhere in the northeastern United States provide important early successional habitat for these same declining bird species (Bramble et al. 1994; King and Byers 2002; Yahner et al. 2002, 2003).

Conservation implications.—Forest management of small, contiguous 1-ha plots to create activity centers for Ruffed Grouse has benefited this species over the past two decades at the Barrens GHMA (McDonald et al. 1994). Intensive forest management on this site also has benefited coexisting early successional songbird species, but these small plots become less suitable as habitat for these species as plant succession progresses (Yahner 1997, Lewis and Yahner 1999). My study has shown, however, that periodic creation of recently cut plots through even-aged management has a positive influence on the breeding bird community, especially early successional species. Furthermore, abundances of woodland species do not appear to be affected detrimentally by intensive management for grouse habitat on a local scale. Although considerable attention has been given to managing extensive forested tracts for woodland bird species, certain tracts of land (e.g., the Barrens GHMA) should be managed specifically as early successional habitats in extensively forested areas (e.g., northcentral Pennsylvania; Askins 2001). This is critical to the conservation of regional populations of early successional bird species, which are among the wildlife experiencing precipitous population declines in recent decades (Brawn et al. 2001). Moreover, this strategy demonstrates that habitat for both early successional and mature forest species can be achieved simultaneously within the same managed forested landscape.

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NESTING AND FEEDING TREE SELECTION IN THE ENDANGERED WHITE-BACKED WOODPECKER, *DENDROCOPOS LEUCOTOS LILFORDI*

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ABSTRACT.—The White-backed Woodpecker (*Dendrocopos leucotos*) is one of the rarest European woodpeckers and its populations have declined markedly during the last century in many European countries. The objective of our study was to investigate the selection of nesting and feeding trees by the subspecies *D. l. lilfordi*, a field not previously investigated. We conducted this study in a mountain area of central Italy characterized by wide and homogeneous tracts of beech- (*Fagus sylvatica*) forested slopes. The rate at which we detected the species was highly correlated with the mean trunk dbh of the stand; the more mature the stand, the greater the number of woodpecker detections. The White-backed Woodpecker was dependent upon trees that were mature, dead, or in an advanced degree of decay for both nesting and foraging. The habitat specialization of the species suggests that forest stand management should promote longer harvesting rotations, preserve dead and decaying trees, create new foraging sites, and prevent excessive fragmentation of forested landscapes. *Received 14 February 2003, accepted 9 June 2003.*

Habitat requirements regarding nesting and feeding sites are important components of habitat selection by birds and are fundamental aspects in the conservation of endangered species, particularly those species that specialize on habitats affected by severe human induced alterations, such as woodlands (Hildén 1965, Cody 1985). Modern forestry has influenced bird populations in many ways since the early 1900s, and woodpecker species are particularly vulnerable because of their dependence upon dead and decaying wood for foraging sites (Aulén 1991).

Woodpecker nest sites may be quantitatively described by the properties of the nesting tree, the nest hole, and the trees used as feeding sites (Hågvar et al. 1990). The White-backed Woodpecker (*Dendrocopos leucotos*) is one of the rarest European woodpeckers (Wesolowski 1995) and its vulnerability to extinction appears to be acute (Spiridonov and Virkkala 1997, Krams 1998). Populations of this species have declined in many countries, especially in Finland (Virkkala et al. 1993, Martikainen et al. 1998), Germany (Scherzinger 1990), Norway (Håland and Ugelvik 1990), Poland (Wesolowski and Tomialojć 1986), Russia (Nazarova 1977), Spain (Fernández et al. 1994), and Sweden (Aulén 1986, 1988) where it is considered an endangered species living in isolated populations (Ahlén et al. 1978). This species, together with the Lesser Spotted (*D. minor*) and the Middle Spotted (*D. medius*) woodpeckers, was classified by Angelstam and Mikusinski (1994) as the northern European woodpecker species most sensitive to change in forest structure and composition. This is due to the fact that the White-backed Woodpecker (1) is an insectivorous forest specialist (Mikusinski and Angelstam 1998a), foraging mainly on woodboring and bark-living insects in the deadwood of deciduous trees (Ahlén et al. 1978, Martikainen et al. 1998), and (2) nests in mature, dying, or dead trees (Aulén 1988, 1991; Hågvar et al. 1990; Krams 1998). Both of these elements have been affected by the decreasing amount of mature stands of deciduous forests upon which the species depends, due to intensive forestry management (Aulén 1988, Håland and Ugelvik 1990, Virkkala et al. 1993, Fernández and Azkona 1996, Martikainen et al. 1998, Mikusinski and Angelstam 1998b, Carlson 2000).

In Italy, the subspecies *lilfordi* is considered "vulnerable" by Pinchera et al. (1997) and "endangered" by Calvario et al. (1999), but its status and distribution is unknown within its very limited range (southern Europe, Tur-

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key, Caucasus, and Transcaucasia; Cramp and Simmons 1985). In its Italian range this species is very restricted, probably as a consequence of a glacial relict and its association with several specific structures of beech (*Fagus sylvatica*) forests, which are limited in availability (Pinchera 1997). This factor, together with the territory size of the species, results in low densities and sensitivity to environmental changes (Pinchera and Pellegrini 1999). The conservation of this subspecies is therefore closely related to future forest policy of Apennines beech woods, which determines the age structure of forests. Consequently, studies of nest and feeding site selection, which may influence the distribution and density of this subspecies, are urgently required.

The information available for this subspecies is scarce and limited to its distribution and breeding biology; e.g., there is no information about the present population size (Castiglia et al. 1976; Bernoni 1994; Costantini and Melletti 1992, 1994; Costantini et al. 1993, 1995). The objectives of our study were to investigate nesting and feeding tree selection by this woodpecker, and to gain information useful for the conservation of the species and the management of forested habitats upon which it depends for breeding and foraging.

STUDY AREA AND METHODS

We conducted this study from 1997 to 1999 in a mountain area of the central Apennines between the regions of Latium and Abruzzi (Simbruini-Ernici massif; 42° 06′ N, 13° 04′ E; altitude range: 900–1,800 m). Wide and homogeneous tracts of beech-forested slopes dominated the study area with grazing and fallow farmland in the valleys. Above 1,900 m, high altitude pastures replace forests. Depending upon soil conditions and microclimate, beech may be associated locally with Sycamore (*Acer pseudoplatanus*), Italian maple (*A. opalus*), common yew (*Taxus baccata*), and limited patches of silver fir (*Abies alba*). The typical forest regeneration system in this area was the shelterwood system, which is characterized by harvest of the mature stand in successive cuttings (Peterken 1996). Forestry operations generally are carried out from mid-September to mid-April, but occasionally may take place during late spring and summer. Harvest units are about 10 ha in size and harvests generally are based on a 20- to 25-year rotation interval (Sulli and Bernoni 1993). Dead and decaying trees, which have less production value, generally are left unharvested.

Locating woodpeckers.—We determined the presence of the White-backed Woodpecker by eliciting responses to playback of taped call notes (Cramp and Simmons 1985) during February and March, the two months preceding egg laying, when the birds are most likely to respond (Aulén 1988, Costantini and Melletti 1992). This is a common and efficient method to detect the presence of woodpeckers due to the rapid response of the species to conspecific calls (Müller 1982; Dentesani 1990; Costantini and Melletti 1992, 1994; Fernández and Azkona 1996). To detect woodpeckers and to obtain information on the distribution of the species with regard to forest structure, we established transects in all of the various ages within the stands (from about 20 years, the minimum age of coppices in our study area, to old growth stands of >100 years). We used aerial photographs, from which it was possible to estimate the age of forest patches on the basis of the canopy dimensions and their proximity (Penteriani and Faivre 1997), to establish transects such that they covered the various tree age classes in approximately equal proportion.

Three times during the same breeding season (1997) we sampled an overall length of 30.7 km of transects of a large contiguous forested area. We stopped and played the taped calls every 300–500 m for a total duration of 4.5 min at each stop. We performed each playback session from sunrise to noon. To avoid overestimating the presence of this highly mobile species (Aulén 1988), we counted two individuals only when two successive responses were obtained >1 km apart (Cramp and Simmons 1985). Following the vocal contact with an individual, we searched for occupied nest trees and recent feeding trees in the stand where we obtained the response. A feeding tree was considered to belong to the White-backed Woodpecker only after direct observations of individuals foraging there (Costantini et al. 1995).

To test for a possible relationship between White-backed Woodpecker presence and the age of the stands, we calculated the mean

trunk diameter at breast height (dbh) of trees in the stand in which we elicited a response (it always matched the nesting stand). We estimated mean stand dbh from the first five trees that we found between the playback point from which we obtained the bird response and the approximate direction of the woodpecker call. The only restriction to tree sampling was that the distance between successive sample trees was ≥100 m to avoid collecting data that could be spatially autocorrelated.

Nesting and feeding tree selection.—To investigate nest tree selection, we compared nesting trees (n = 40) to an equal number of control trees. We chose control trees randomly, but in the same stand as each nest tree (see Penteriani et al. 2001 for details), and of a dbh equal to the mean dbh of nesting trees. Thus, our control sample represented the trees available for the species. We characterized nest and control trees with seven variables: altitude (m above msl), dbh, height of the tree, height of the trunk, height of the nest hole, nest hole position (three categories: on the portion of the trunk below the canopy, in the canopy, on a branch), and degree of decay (three categories: dead tree with softened wood, live tree with evidence of decay in several places, live tree without evidence of decay or only a few dead branches).

Similarly, to investigate feeding tree selection, we compared feeding trees (n = 61) to an equal number of control trees chosen as described above. We characterized feeding and control trees with seven variables: percentage of trunk covered by bark, bark condition (two categories: intact and partially sloughed off the trunk), dbh, tree height, trunk height, and degree of decay (as for the nesting tree).

Statistical analyses.—To avoid pseudoreplication, we used only one nesting tree and one feeding tree per breeding pair for all analyses. We used a linear regression to evaluate the relationship between dbh and presence of the White-backed Woodpecker (i.e., the frequency of detection). We divided the mean stand dbh into five classes: <20 cm, 21–30 cm, 31–40 cm, 41–50 cm, and >50 cm. We used a discriminant function analysis (DFA) to detect possible differences in nesting and feeding tree structure between those used by the species and the control trees. We used χ^2 analysis to test the significance of the site classification established by the DFA procedure (Sokal and Rohlf 1995), and Mann-Whitney U-test to compare features of nesting and feeding trees used by the woodpeckers with those of the control trees. We used the χ^2 test to analyze the frequencies of use of several categories considered for nesting and feeding trees. When data were not normally distributed, they were $\log_e$, square-root, or arcsine square-root transformed prior to parametric tests (Sokal and Rohlf 1995). If the data still did not approach normality, nonparametric tests were employed. All tests were two-tailed and we set statistical significance at $P < 0.05$. All tests were computed using SPSS 10.0 (Norusis 1992).

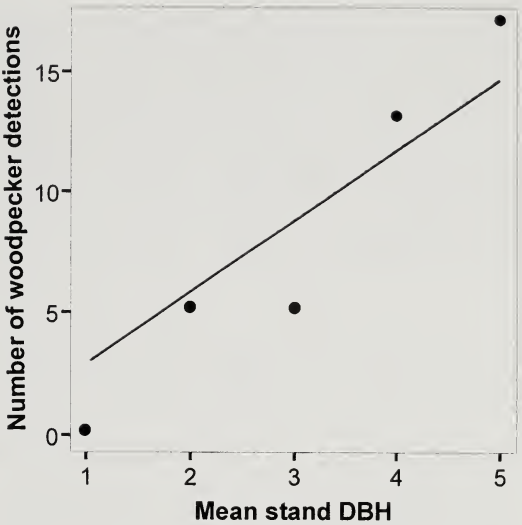

FIG. 1. Frequency of contacts with the White-backed Woodpecker (*Dendrocopos leucotos lilfordi*) increased with maturity of forest stands in beech (*Fagus sylvatica*) woodlands of Central Italy. The degree of stand maturity is expressed by five dbh classes: 1 = <20 cm, 2 = 21–30 cm, 3 = 31–40 cm, 4 = 41–50 cm, 5 = >50 cm.

RESULTS

Frequency of detections.—The frequency of detections of White-backed Woodpeckers was highly correlated (r^2 = 0.94) with the mean stand dbh ($t_{1,3}$ = 6.75, P = 0.007). The more mature the stands were, the greater was the number of woodpecker detections (Fig. 1).

Nesting tree selection.—White-backed

TABLE 1. Nesting trees (n = 40) of the White-Backed Woodpecker differed from control trees (n = 40) in beech stands of Central Italy, 1997–1999.

	Nesting trees				Control trees		Mann Whitney U-test	
	$\bar{x}$	SD	Minimum	Maximum	$\bar{x}$	SD	Z	P
Altitude (m above msl)	1,250	165	900	1,645	1,406	100	4.50	0.0001
Trunk dbh (cm)	51	18	23	129	21	20	5.71	0.0001
Height of tree (m)	25	6	5	28	21	12	3.45	0.0010
Height of trunk (m)	18	5	4	22	16	5	0.64	0.5200

Woodpeckers bred across a broad altitudinal range, in cavities generally located in the middle of the trunk of old trees (mean = 10.5 m ± 2.8 SD, range 2.3–12.0 m, n = 40), characterized by large dbh values (Table 1). They used mainly live trees without evidence of decay (40.0%), followed by dead trees (32.5%), and live trees with evidence of decay in several places (27.5%). The observed use of the above types of trees was significantly different from that expected (χ^2 = 12.2, df = 2, P = 0.007). Seventy-five percent (i.e., 30 of 40) of the nest holes were in the portion of the trunk below the canopy, whereas the remaining 25% were within the canopy (χ^2 = 10.0, df = 1, P = 0.002). The most frequent orientation of the slope used for nesting was toward the northwest (n = 12), followed by southwest and west (n = 8 each), southeast (n = 7), northeast and north (n = 2 each), and south (n = 1; χ^2 = 25.6, df = 7, P = 0.001). The discriminant function analysis significantly (P = 0.0001) distinguished between nesting and control trees. Trees used for nesting generally were greater in height and dbh than control trees, and woodpeckers nested on trees located at lower altitudes (Table 1). The discriminant equation was D = 3.579 − 0.004(altitude) + 3.706(dbh) − 0.028(tree height). The model correctly classified 35 (87.5%) of the nesting trees and 39 (97.5%) of the control trees for an overall error rate of 7.5%.

Feeding tree selection.—White-backed Woodpeckers foraged primarily in mature trees characterized by variable bark conditions (mean = 62.9% ± 35.7 SD, range 0–100%, n = 61) and large dbh as feeding sites (Table 2). The birds mainly used live (43%) and dead (41%) trees, followed by trees with dead branches (16%). The observed use of the above types of trees was significantly different from that expected (χ^2 = 7.9, df = 2, P = 0.020). Of trees used for foraging, 80% were trees with the bark partially removed from the trunk, and the remaining 20% were trees showing no sign of weakness (χ^2 = 22.4, df = 1, P = 0.0001). The discriminant function analysis significantly (P = 0.0001) distinguished between feeding and control trees. Trees used for feeding, although shorter than control trees, generally were greater in trunk height and dbh (Table 2). The discriminant equation was D = −1.221 − 0.213(tree height) + 4.420(dbh) + 0.209(trunk height). The model correctly classified 59 (96.7%) of the feeding trees and 58 (95.1%) of the control trees for an overall error rate of 4.1%.

DISCUSSION

Frequency of contacts.—The correlation of mean stand dbh (as an index of stand maturity) and frequency of contacts of the White-backed Woodpecker suggest a dependence upon mature stands. A similar relationship be-

TABLE 2. Feeding trees (n = 61) of the White-Backed Woodpecker differed from control trees (n = 61) in beech stands of Central Italy, 1997–1999.

	Feeding trees				Control trees		Mann Whitney U-test	
	$\bar{x}$	SD	Minimum	Maximum	$\bar{x}$	SD	Z	P
Trunk dbh (cm)	41	19	16	130	20	10	5.54	0.0001
Height of tree (m)	12	6	1	25	19	3	5.96	0.0001
Height of trunk (m)	8	4	1	18	7	3	2.20	0.0280

tween woodpecker occurrence and stand age (characterized by dbh) was reported by Bernoni (1994), and by Pinchera (1997) who never detected the species in coppices (i.e., early successional forest stands of small-diameter stems, formed from the sprouting of new young trees from existing stumps and root stock of harvested trees). Other researchers examining woodpecker presence and forest structure consistently found similar associations with the oldest stages of stand growth, characterized by large numbers of old trees and large dbh values (Fernández and Azkona 1996, Mikusinski and Angelstam 1998a, 1998b). Costantini and Melletti (1992) demonstrated that the distribution of White-backed Woodpeckers in the study area was strictly related to the heterogeneity of the stand structure (i.e., stands with trees highly diversified in age and decay conditions).

Nesting tree selection.—Although this species occupied a large altitudinal range, as reported by Fernández et al. (1994) in Spain and Grangé (1993) in France, the woodpeckers in our study used the highest elevation belt of the Apennines beech forest for breeding. This pattern, also observed by Pinchera (1997), could not be random for the beech forest of the Italian Apennines. In fact, the highest belts of these forests (about 1,300–1,600 m above msl) correspond to areas with the most of mature trees and oldest stands, due to the concentration of past timber harvests in the more accessible lower belts of forest, and a less favorable climate for beech above about 1,600 m (Penteriani and Faivre 1997). A similar influence of the combination of human and climatic factors on the altitudinal distribution of this woodpecker also was suggested by Fernández and Azkona (1996).

Our analyses confirmed the selection of mature trees with large dbh values for excavating nest holes, as reported by Hågvar et al. (1990). Use of younger stands has been reported only by Krams (1998), who found ≤23% of the nesting trees were in mature stands. The author attributed this pattern to the relatively young age of the forest stands in his study area, which is considered a cause of the decline of the species in the Latvia population. The apparent dependence of this species upon large trees also could reflect that large trees are more likely than small trees to contain dead wood.

The White-backed Woodpecker usually uses dead trees for excavating its nest hole (Aulén 1988, Hågvar et al. 1990, Krams 1998), although in our study area we detected a relatively frequent use of fully vital trees, which also was observed by Hågvar et al. (1990) and Pinchera (1997). Although the frequent use of vital trees might be related to their availability, this finding supports the hypothesis that, depending on the specific hardness of each tree species, some trees may be used even if not dead or in an advanced degree of decay (Aulén 1988). However, we cannot discard the possibility that apparently healthy trees may be partially weakened by fungi; early stages of fungi parasitism usually are difficult to detect because of the absence of external trunk damage, even if internal wood is already softened by decay (T. Wesolowski pers. comm.).

The mean nest hole height was the same as reported by Pinchera (1997) and Hågvar et al. (1990), and similar to the most frequent height reported by Kram (1998), although a greater mean height (17.8 m) was reported by Wesolowski and Tomialojć (1986) in Poland, attributed to the height of the trees available in Bialowieza. White-backed Woodpeckers appear to select western and especially northwestern slopes, which correspond to the best exposure for beech growth (Penteriani and Faivre 1997).

Feeding tree selection.—Similar to nesting trees, the feeding trees selected had large dbh values, although their mean height was less than control trees. This result was influenced by the fact that several trees used as feeding sites were stumps, broken by wind or snow, or destroyed by insects and fungi. Our data lend further support to the hypothesis that White-backed Woodpeckers, which specialize on the larvae of xylophage insects, are dependent upon dead and highly decayed trees that attract this specific food resource (Matsuoka 1979, Aulén 1991, Mikusinski and Angelstam 1998b); such trees also characterize the nesting stands of this woodpecker (Aulén 1988, Fernández et al. 1994, Pavlík 1999). The importance of dead trees also was emphasized by Carlson (1998), who demonstrated a positive relationship between the density of dead

trees and feather growth in the White-backed Woodpecker, the latter being considered an index of the bird's nutritional condition. Nevertheless, as also suggested by Carlson (1998), the relatively large number of living trees we found as feeding sites is not surprising, considering the insect-rich dead and decaying branches they can carry, which make them attractive to White-backed Woodpeckers (Aulén 1988).

Conservation and management implications.—The White-backed Woodpecker declined markedly during the last century in many European countries, particularly due to habitat loss associated with timber harvesting. Moreover, the endangered subspecies *lilfordi* represents a very localized endemic of the southern European montane forests (Voous 1947). The data we present corroborates the nesting and feeding site specialization of this species, and leads us to make the following recommendations. (1) Timber harvesting rotations, currently 20–25 years in our study area and other European countries, should be lengthened. (2) Older dead and decaying trees within each stand should be preserved; as these trees are of little harvest value, such preservation represents virtually no economic loss. (3) The possibility of creating new foraging sites by killing deciduous trees, consequently increasing insect abundance, should be evaluated. Finally, (4) fragmentation of the forest should be prevented to avoid reducing the original woodpecker population to isolated subpopulations confined to small patches of suitable habitat. Such fragmentation, along with habitat degradation, probably has increased the White-backed Woodpecker's susceptibility to extinction (Aulén 1988, Tiainen 1990, Carlson and Aulén 1992, Krams 1998).

Until recent years, the Apennines forests of Central Italy provided favorable and unfragmented habitat for the species, undoubtedly one of the most important in Europe. This region supported extensive beech forests that represent optimal habitat for a species requiring 50–100 ha of deciduous forest for a pair to survive (Aulén 1988, Scherzinger 1990, Virkkala et al. 1993). These stands were relatively intact because of the difficulty in harvesting stands at high altitudes with a limited number of logging trails. Although there is no information about the effective population size, density, and population trends, the survival of the White-backed Woodpecker in Central Italy is uncertain because timber harvesting currently is removing the essential habitat. Despite the need for urgent measures of forest management to preserve the subspecies *lilfordi* in Italy, timber harvesting remains uncontrolled in several protected areas, and in some cases extensive logging of old-growth stands occurs with the tacit consent of the local authorities.

Finally, the White-backed Woodpecker can be considered an umbrella species (*sensu* Fernández et al. 1994, Martikainen et al. 1998). Such status not only facilitates efforts to preserve this woodpecker, but also other species less conspicuous or less well known to the public. For example, many threatened beetle species inhabit the same habitat as the White-backed Woodpecker (Martikainen et al. 1998). Also, the extension of timber rotation age beyond the present 20–25 yrs could prevent genetic drift and inbreeding depression in tree populations that influence tree vitality and forest health (Scoppola 1999).

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TEMPORAL PATTERNS IN THE DIET AND FOOD PARTITIONING IN IMPERIAL CORMORANTS (*PHALACROCORAX ATRICEPS*) AND ROCK SHAGS (*P. MAGELLANICUS*) BREEDING AT BAHÍA BUSTAMANTE, ARGENTINA

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ABSTRACT.—We studied the diet of Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*P. magellanicus*) at Bahía Bustamante, Argentina, between 1992 and 1994. We analyzed pellet casts (1887 from Imperial Cormorants and 799 from Rock Shags) and regurgitations of stomach contents (260 from Imperial Cormorants and 24 from Rock Shags). Imperial Cormorants and Rock Shags fed on at least 22 and 21 different types of prey, respectively. The main prey species during all study years were fish: *Engraulis anchoita* for Imperial Cormorants and *Patagonothen* sp. for Rock Shags. For both species, the consumption of the main food categories as estimated by pellet analysis was similar among years. A significant relationship was found between Imperial Cormorant and Rock Shag diets during the three years, while the diet overlap index was relatively high. During all years, Imperial Cormorants consumed a significantly larger proportion of pelagic or demersal fish than did Rock Shags, while Rock Shags consumed benthic fish in a greater proportion than did Imperial Cormorants. Mean maximum diving depth, determined using capillary tube depth gauges, of Imperial Cormorants (24.4 m ± 18.8 SD) was significantly greater but more variable than that of Rock Shags (9.3 m ± 4.1 SD). *Received 29 October 2002, accepted 10 March 2003.*

Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*Phalacrocorax magellanicus*) are widely distributed along the Argentine coast (Yorio et al. 1998). The Imperial Cormorant is a relatively abundant seabird, with nearly 50,000 breeding pairs in colonies of up to several thousand nests, whereas the Rock Shag has a population of >7,000 pairs distributed in relatively small colonies (Yorio et al. 1999). Despite the wide distribution of these cormorant and shag populations, relatively little is known about their diet and food partitioning. Few studies on their diets have been conducted along the Patagonian coast, and these have focused on only a single species and breeding season (Malacalza et al. 1994, 1997; Gosztonyi and Kuba 1998) or have been based on a small sample size (Punta et al. 1993). Foraging patterns and diving behavior have been reported at only two Patagonian sites (Quintana 1999, 2001; Sapoznikow and Quintana 2003). At most breeding locations in Patagonia, these two species share the same colony sites (Punta 1989, Gandini and Frere 1998, Schiavini et al. 1998). However, no studies yet have quantitatively analyzed food partitioning between these congeneric cormorant species. The objectives of this study were to (1) analyze the diet and maximum diving depths of breeding Imperial Cormorants and Rock Shags during three years at Bahía Bustamante, Golfo San Jorge, (2) compare the results with those previously obtained at other Patagonian locations, (3) analyze diet variation among years and stages of the breeding cycle, and (4) assess food partitioning between the two species.

METHODS

Diet sampling and analysis.—We studied the diets and diving behavior of Imperial Cormorants and Rock Shags in the Bahía Bustamante area (45° 05′ S, 66° 28′ W to 45° 13′ S, 66° 30′ W), Golfo San Jorge, Chubut, Argentina. We collected pellets in active nests (1,887 samples from Imperial Cormorants and 799 from Rock Shags) and obtained regurgitated stomach contents from birds when we approached their nests (260 samples from Imperial Cormorants and 24 from Rock Shags). Samples were gathered mostly at colonies of both species at Isla Galiano. In addition, we obtained diet samples at other breeding sites, including Islas Lobos, Isla Ezquerra, Isla Ver-

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naci Este, Isla Vernaci Oeste, and Isla Viana, all 6.5–11 km from Isla Galiano.

We collected samples from early November to February in 1992 and from October to February in both 1993 and 1994. We visited colonies at 1- to 4-week intervals during 1992 and 1994, and at 1- to 2-week intervals during 1993. During each visit we noted the breeding status of nests within the study areas. We froze regurgitates and dried pellets until we examined them in the laboratory. We examined each sample with a microscope (21× magnification) and identified food remains to the lowest taxonomic level possible, using fish otoliths, squid beaks, crustacean shell fragments and chelae, mollusks shell fragments, polychaete mandibles and chetae, and echiurid remains. We identified prey with the aid of published guides (Torno 1976, Menni et al. 1984, Clarke 1986, Boschi et al. 1992) and a reference collection obtained from the study area.

For each prey species, we recorded the percentage of occurrence from pellets and percent mass from regurgitates. For the analysis of seasonal variation in diet we used only pellet samples, and grouped prey into five prey categories (fish, crustacean, cephalopod, echiurid, and polychaete). We divided the breeding cycle into four stages: prelaying, incubation, young chicks (chicks up to the first molt, approximately 4 weeks of age), and old chicks (chicks between the first molt and fledging).

Diving behavior.—We studied maximum diving depth of Imperial Cormorants and Rock Shags with capillary tube depth gauges during 1994. We attached depth gauges (Burger and Wilson 1988) on 162 Imperial Cormorants and 90 Rock Shags. The gauges were taped to wing feathers and we retrieved them mostly (71.6%) within 24 h of deployment (83.2% within 48 h). After recovering a gauge, we measured to the nearest 0.05 mm the length of the tube still covered with indicator powder; gauges that were difficult to read were eliminated from the analysis. We calculated maximum depth with the equation: $D_{max} = 10.08 (L_i/L_d - 1)$, where D_{max} is the maximum depth attained (in m), L_i is the initial length of undissolved indicator powder (in mm), and L_d the length on recovery (in mm) (Burger and Wilson 1988).

Statistical analysis.—We used *G*-tests to analyze the variation of each food category throughout the breeding cycle and to conduct comparisons among locations and between years. We used ANOVAs to analyze differences in consumption among prey categories and the number of prey taxa per pellet among stages of the breeding cycle. To compare diets of Imperial Cormorants and Rock Shags, we used a Spearman correlation coefficient, ranking prey according to their frequency of occurrence (Ashmole and Ashmole 1967). We evaluated diet overlap between both species using the Morisita index. We used nonparametric tests whenever underlying assumptions were not met.

RESULTS

Imperial Cormorant diet.—Pellet analysis indicated that Imperial Cormorants fed on a wide variety of prey during all years, including at least 22 different types of prey (Table 1). Fish were the most frequently identified prey during the three years, followed by crustaceans and cephalopods. We identified 20 prey types from regurgitate samples, including the crustacean *Peisos petrunkevitchi*, which was not detected in pellets. The main prey species during all study years was the fish *Engraulis anchoita*. Fish consumption, measured as mean wet mass, during the three years was significantly greater than that of crustaceans, cephalopods, echiurids, and polychaetes (ANOVA $F_{5,423} = 16.2$, $P = 0.0001$). The percentage of fish by wet mass was over 70% in all years (Table 1).

Consumption of food categories as estimated by pellet analysis was similar among years ($G_4 = 3.49$, $P = 0.48$). During 1993, consumption of fish as estimated by pellet analysis was similar among all stages of the breeding cycle ($G_3 = 6.16$, $P = 0.10$), while the consumption of prey from the rest of the food categories throughout the season was highly variable (all $G_3 > 9.0$, all $P < 0.05$; Fig. 1). During 1994, consumption of fish, mollusks, and crustaceans was similar among breeding stages (fish: $G_3 = 2.60$, $P = 0.46$; mollusks: $G_3 = 1.10$, $P = 0.78$; crustaceans: $G_3 = 4.47$, $P = 0.21$), while the proportion of polychaetes and echiurids in the diet varied throughout the season (polychaetes: $G_3 = 13.32$, $P = 0.004$; echiurids: $G_3 = 11.07$, $P = 0.011$; Fig. 1). The number of prey taxa per pellet increased dur-

TABLE 1. Prey consumed by Imperial Cormorants at Bahía Bustamante, Argentina, 1992–1994, obtained by pellet and regurgitate analysis. Sample size is in parentheses.

Taxa	Percentage occurrence in pellets			Percent fresh mass in regurgitates		
	1992 (1,350)	1993 (275)	1994 (262)	1992 (95)	1993 (115)	1994 (50)
Fish	93.3	96.0	96.6	72.3	71.8	79.0
Engraulis anchoita	58.4	42.5	54.2	56.3	28.1	30.8
Patagonothen sp.	43.2	41.5	45.4	6.7	9.2	13.5
Ribeiroclinus eigenmanni	45.3	28.4	31.3	1.8	9.3	1.7
Raneya brasiliensis	5.2	33.5	52.7	—	3.9	12.5
Agonopsis chiloensis	3.9	20.0	24.8	0.3	0.2	0.4
Odontesthes smitti	12.2	45.8	46.6	—	3.9	1.0
Odontesthes incisa	11.9	14.6	17.9	—	0.3	—
Merluccius hubbsi	4.6	37.1	43.9	0.8	11.9	10.1
Eleginops maclovinus	0.7	12.4	17.9	—	—	—
Ramnogaster arcuata	1.7	9.1	14.1	1.7	—	5.0
Percophis brasiliensis	1.3	1.1	5.0	—	—	—
Genypterus blacodes	1.5	7.6	24.4	1.5	4.3	—
Stromateus brasiliensis	0.4	—	—	—	—	—
Unidentified fish	0.9	0.4	—	3.2	0.7	4.0
Crustaceans	69.8	55.1	69.8	8.2	12.5	10.8
Betaeus truncatus	58.8	34.5	49.6	1.4	4.4	4.9
Peltarion spinosulum	17.9	17.1	16.0	0.7	5.9	3.4
Pleoticus muelleri	1.2	3.3	8.4	0.7	0.3	—
Munida subrugosa	2.7	12.0	14.5	4.5	1.4	1.2
Lithodes santolla	—	5.8	9.2	—	—	1.3
Peisos petrunkevitchi	—	—	—	0.9	0.5	—
Cephalopods	57.5	60.9	61.8	6.5	7.0	6.5
Octopus sp.	47.4	33.5	35.5	5.2	5.9	3.5
Loligo gahi	16.3	38.2	40.8	1.3	1.1	3.0
Echiurids	44.2	35.6	39.7	4.0	3.3	1.5
Polychaetes	74.2	41.1	48.5	2.6	2.6	1.8
Aphrodita sp.				—	—	—
Polinoe sp.				—	—	—
Unidentified prey	2.7	0.4	1.1	6.4	2.8	0.4
Total mass (g)				3,722.1	7,143.8	4,806.5

ing the breeding season, reaching maximum values during the early chick stage (1993: ANOVA $F_{3,270} = 14.5$, $P < 0.0001$; 1994: ANOVA $F_{3,252} = 7.2$, $P = 0.0001$; Table 2).

Rock Shag diet.—Pellet analysis indicated that Rock Shags fed on a wide variety of prey during all years, including at least 21 different types of prey; fish were the most frequently identified prey during the three years, followed by polychaetes and crustaceans (Table 3). The main prey species were *Patagonothen* sp. and *Ribeiroclinus eigenmanni*. We identified 20 prey types from the regurgitates. Fish consumption, measured as mean wet mass during both 1993 and 1994, was significantly greater than that of crustaceans, cephalopods, echiurids, and polychaetes (ANOVA $F_{4,64} = 2.7$, $P = 0.039$). The percentage of fish wet mass was over 90% in 1994, but was only about 40% in 1993 (Table 3). Regurgitate analysis indicated that *Patagonothen* sp. was the main prey species in both years (Table 3).

The consumption of the food categories as estimated by pellet analysis was similar among years ($G_4 = 1.55$, $P = 0.82$). During 1993, the consumption of fish, mollusks, and echiurids varied significantly among stages of the breeding cycle (fish: $G_3 = 9.34$, $P = 0.025$; mollusks: $G_3 = 11.74$, $P = 0.008$; echiurids: $G_3 = 8.50$, $P = 0.037$), while the consumption of crustaceans and polychaetes was similar (crustaceans: $G_3 = 6.67$, $P = 0.083$; polychaetes: $G_3 = 0.29$, $P = 0.96$; Fig. 2). During 1994, the consumption of echiurids throughout the season was highly variable ($G_3 = 11.49$, $P = 0.009$), while no significant sea-

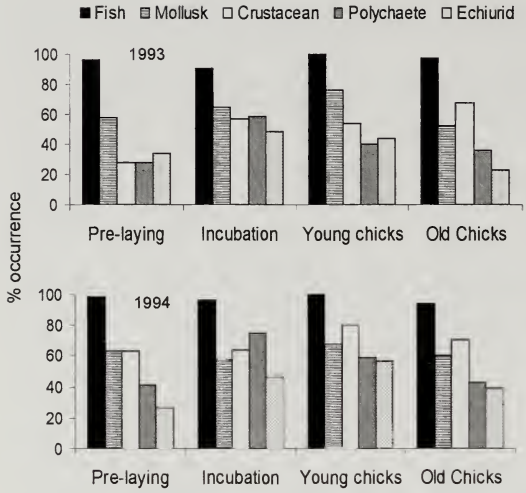

FIG. 1. Seasonal variation in the main prey types of Imperial Cormorants at Bahía Bustamante, Argentina, during 1993 and 1994.

sonal variation was detected for the other food categories (all $G_3 < 7.69$, all $P > 0.05$; Fig. 2). During 1993 and 1994, the number of prey taxa per pellet increased with the breeding season, reaching maximum values during the late chick stage (1993: ANOVA $F_{3,236} = 9.0$, $P < 0.0001$; 1994: ANOVA $F_{3,188} = 4.2$, $P < 0.007$; Table 2).

Comparison between Imperial Cormorant and Rock Shag diet.—Imperial Cormorants and Rock Shags shared most of the prey types. All prey types identified in Rock Shag samples also were consumed by Imperial Cormorants. A significant correlation was found between their diets during all three years (1992: $r_s = 0.86$, df = 19, $P = 0.0001$; 1993: $r_s = 0.73$, df = 19, $P = 0.001$; 1994: $r_s = 0.70$, df = 19, $P = 0.002$), and the diet overlap index was relatively high (1993: C = 0.67 and 1994: C = 0.69).

During 1993 and 1994, Imperial Cormorants consumed a significantly larger proportion of pelagic or demersal fishes than did Rock Shags (1993: $\chi^2 = 10.5$, df = 1, $P = 0.001$; 1994: $\chi^2 = 20.1$, df = 1, $P < 0.0001$), while Rock Shags consumed benthic fishes in a greater proportion than did Imperial Cormorants (1993: $\chi^2 = 36.2$, df = 1, $P < 0.0001$; 1994: $\chi^2 = 9.8$, df = 1, $P = 0.002$; Table 4).

Diving behavior.—A total of 41% and 31% of depth gauges deployed on Imperial Cormorant and Rock Shags, respectively, were recovered. Mean maximum depth of Imperial Cormorant (24.4 m ± 18.8 SD, range = 5.7–78.1 m, $n = 67$) was significantly greater than that of Rock Shags (9.3 m ± 4.1 SD, range = 3.8–21.0 m, $n = 28$; Mann-Whitney $Z = 5.5$, $P < 0.0001$; Fig. 3). Maximum depths attained by Imperial Cormorants were more variable than those of Rock Shags (CV: 0.77 versus 0.44, respectively).

DISCUSSION

Diet analyses showed that fish were the main prey consumed by both Imperial Cormorants and Rock Shags at Bahía Bustamante. Our results agree with those obtained for both species at other locations along the northern Patagonian coast. Malacalza et al. (1994) and Gosztonyi and Kuba (1998) reported that Imperial Cormorants at Punta León and Punta

TABLE 2. Number of prey taxa per pellet (mean ± SD) of Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994 during the four stages of the breeding cycle. Sample size is in parentheses.

Year and species	Pre-laying	Incubation	Young chicks	Old chicks
1993				
Imperial Cormorant	3.4 ± 1.7 (50)	5.3 ± 2.5 (74)	6.2 ± 2.0 (50)	5.4 ± 2.7 (100)
Rock Shag	4.7 ± 2.2 (80)	5.4 ± 1.9 (35)	6.3 ± 2.2 (85)	6.8 ± 2.5 (40)
1994				
Imperial Cormorant	5.7 ± 2.7 (68)	6.3 ± 2.9 (28)	8.2 ± 2.7 (46)	6.2 ± 3.3 (120)
Rock Shag	5.5 ± 2.0 (70)	5.3 ± 2.0 (19)	5.2 ± 2.2 (28)	6.7 ± 2.9 (75)

TABLE 3. Prey consumed by Rock Shags at Bahía Bustamante, Argentina, 1992–1994, obtained by pellet analysis and regurgitate analysis. Sample size is in parentheses.

Prey	Percentage occurrence in pellets			Percent fresh mass in regurgitates	
	1992 (367)	1993 (240)	1994 (192)	1993 (10)	1994 (12)
Fish	91.9	89.6	93.2	41.4	93.8
Engraulis anchoita	47.0	33.3	38.0	—	16.3
Patagonothen sp.	67.4	69.6	75.0	33.1	43.1
Ribeiroclinus eigenmanni	68.8	62.1	67.7	8.3	9.5
Raneya brasiliensis	1.9	12.5	15.6	—	9.2
Agonopsis chiloensis	11.1	42.1	52.6	—	—
Odontesthes smitti	3.3	35.0	29.7	—	2.4
Odontesthes incisa	7.9	13.3	13.5	—	—
Merluccius hubbsi	1.9	9.6	10.9	—	—
Eleginops maclovinus	2.2	19.2	14.1	—	—
Ramnogaster arcuata	0.8	8.3	7.3	—	—
Percophis brasiliensis	1.4	5.8	3.1	—	—
Genypterus blacodes	0.0	1.3	2.6	—	2.1
Unidentified fish	1.4	—	—	—	11.2
Crustaceans	70.6	64.2	67.7	21.0	6.2
Austropandalus grayi				—	—
Betaeus truncatus	58.2	59.2	65.1	8.1	3.4
Nauticaris magellanica				—	—
Campylonotus vagans				—	—
Peltarion spinosulum	16.9	14.2	16.2	11.4	2.8
Leucippa pentagona				—	—
Pleoticus muelleri	3.3	—	—	—	—
Munida subrugosa	3.0	6.3	3.1	1.5	—
Lithodes santolla	—	—	0.5	—	—
Cephalopods	60.3	55.8	59.9	15.5	—
Octopus sp.	56.3	45.0	50.0		
Loligo gahi	9.5	17.1	17.2	—	—
Echiurids	60.1	39.2	34.4	7.1	—
Polychaetes	84.0	75.4	71.4	15.0	—
Aphrodita sp.				—	—
Polinoe sp.				—	—
Unidentified prey	3.3	0.4	2.1	—	—
Total mass (g)				574.7	524.3

Lobería had similar diets, with fish being the dominant prey. Fish also was the main prey type reported for other species of the "blue-eyed cormorant complex" breeding in other regions (Brothers 1985, Espitalier-Noel et al. 1988, Green et al. 1990, Wanless et al. 1992, Ridoux 1994, Casaux et al. 1997, Favero et al. 1998). Relatively fewer references are available on Rock Shag diet throughout its range, and these show that fish also are their main prey (Bahamonde 1955, Punta et al. 1993, Malacalza et al. 1997).

Previous studies have shown that Imperial Cormorants include a variety of fish species in their diet. At Punta León, diet included seven species, mainly *Triathalassothia argentina* and *Raneya fluminensis*, of which four are common to our study (Malacalza et al. 1994). At Punta Lobería, Gosztonyi and Kuba (1998) found a total of 12 fish species, mostly *Tripterygion cunninghami*, *Engraulis anchoita* and *Patagonothen* sp. Our results in Bahía Bustamante showed a similar number of species, although only half of them are shared by both cormorant populations. Differences also were found in a previous study conducted at Bahía Bustamante based on a relatively small sample size, where a lower number of fish species was reported (Punta et al. 1993). Given the small interannual variability observed in this study, differences observed are likely due to differences in the analytical methods applied in the two studies. During all three years of the present study, crustaceans, ceph-

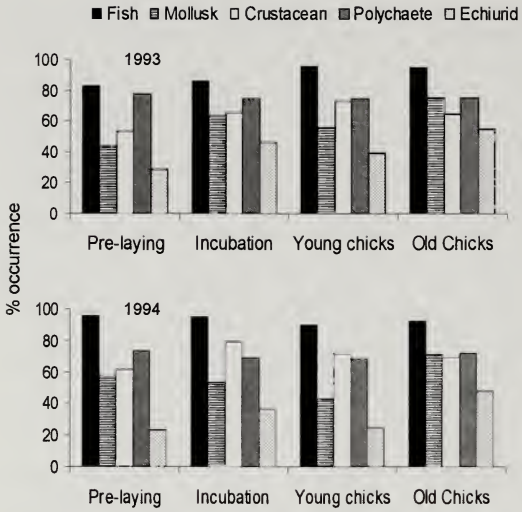

FIG. 2. Seasonal variation in the main prey types of Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994.

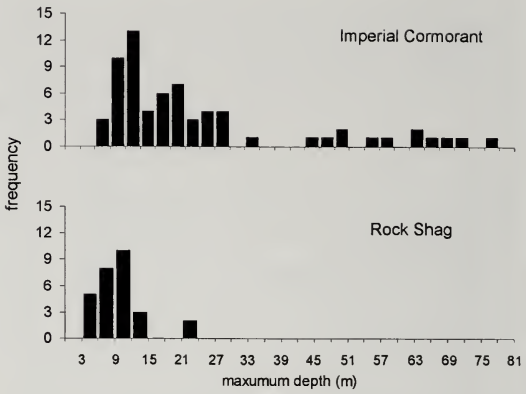

FIG. 3. Frequency distribution of maximum diving depths for Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1994.

alopods, echiurids, and polychaetes comprised the diet of Imperial Cormorants and Rock Shags. However, the proportion of polychaetes in pellet samples of both species may have been overestimated, polychaetes being the result of secondary consumption (Casaux et al. 1995, Johnson et al. 1997).

At Bahía Bustamante, Imperial Cormorants and Rock Shags preyed upon a wide variety of fish and invertebrates found in different coastal habitats, including benthic, demersal, and pelagic areas. Benthic prey included fish found on rocky, sandy, and muddy bottoms. Fish, such as *Patagonothen* sp., *Agonopsis chiloensis* and *Ribeiroclinus eigenmanni*, live in inshore habitats among algae (Gosztonyi and Kuba 1998). Such flexibility in feeding habits also has been reported for other cormorants, and it was argued that this flexibility plays an important role in maximizing cormorant food intake (Grémillet et al. 1998).

Punta et al. (1993) reported changes throughout the breeding cycle in the diet composition of Imperial Cormorants, with an increase in the consumption of fish, particularly *Engraulis anchoita* and nototheniids, and a decrease of crustacean prey as the season progressed. However, no seasonal changes were observed in the consumption of fish by either Imperial Cormorants or Rock Shags during this study. *Engraulis anchoita* schools approach the coast during November and December (R. Fondacaro pers. comm.), and their availability to breeding birds near their colonies may vary among years with oceanic conditions.

This study suggests that Imperial Cormorants and Rock Shags have substantial dietary

TABLE 4. Pelagic (P) and benthic (B) fish preyed upon by Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994 during the four stages of the breeding cycle. Values are frequency of occurrence.

	Pre-laying		Incubation		Young chicks		Old chicks		Total	
Year and species	P	B	P	B	P	B	P	B	P	B
1993										
Imperial Cormorant	96	15	81	60	84	54	93	46	89	45
Rock Shag	61	83	80	67	85	88	76	79	75	82
1994										
Imperial Cormorant	94	52	100	67	100	76	96	42	96	53
Rock Shag	69	91	72	67	88	80	80	81	76	83

overlap, i.e., food partitioning is not demonstrated. However, ecological segregation in seabirds may be achieved through a combination of differences in diet, feeding range (both vertical and horizontal), and feeding behavior (Ashmole and Ashmole 1967, Ridoux 1994, Croxall et al. 1997). Among related species such as the Imperial Cormorant and Rock Shag, overlap in diet may be expected (Ridoux 1994), but prey size may be a more important mechanism of dietary segregation than prey type. Several studies have found differences in prey sizes between congeneric species (Ashmole and Ashmole 1967, Hulsman 1988, Fasola et al. 1989). The mean body mass of Imperial Cormorants is greater than that of Rock Shags (2.3 versus 1.5 kg; F. Quintana unpubl. data), and at Golfo San Jorge preliminary results suggest that the former feeds on larger prey (GP unpubl. data). Further studies should examine the role of prey size in the possible partitioning of food resources between the two species.

Differences in foraging range also have been found to be important in the segregation of seabird communities (Hulsman 1988, Adams and Brown 1989, Weimerskirch et al. 1988, Croxall et al. 1997). Our results on diving behavior show that Imperial Cormorant diving depth was significantly greater than that of Rock Shags, suggesting that the former species is capable of foraging on benthic prey farther away from the colonies and thus may have a wider foraging range. Recent research supports this hypotheses, as Sapoznikow and Quintana (2003) found that although both species generally foraged close to their colonies, some Imperial Cormorants traveled farther offshore during their foraging trips. Imperial Cormorants also have been observed feeding farther offshore than Rock Shags in waters around the Malvinas (Falkland) Islands (Thompson 1989, White at al. 1999).

Feeding habits also may contribute to the partitioning of food resources. Despite the similarities in the diets of Imperial Cormorants and Rock Shags, differences between the two species were found in the proportion of fish they obtained from different habitats, with Imperial Cormorants consuming a larger proportion of pelagic and demersal fish prey, particularly *Engraulis anchoita*. At Bahía Bustamante, Imperial Cormorants and Rock Shags mainly foraged individually, although the former species was observed foraging in groups on several occasions (Punta et al. 1993). Group foraging behavior was reported extensively for seabirds which prey upon dense schools of pelagic fish (Jordán 1967, Duffy 1983, Schreiber and Clapp 1987) and, consistent with this, Punta et al. (1993) reported that group foraging became more frequent at approximately the same time that *Engraulis anchoita* started to occur in diet samples. The observed differences in the proportion of pelagic and benthic prey between cormorants and shags may be the result of differences in foraging habits, with Imperial Cormorants perhaps having a wider feeding range, making greater use of the water column, and being able through group feeding to prey more effectively and in an opportunistic way upon dense schooling fish.

An overlap in diet also may reflect good feeding conditions near the colonies during the study. Substantial overlap in diet has been reported in seabird breeding assemblages (Furness and Barret 1985, Croxall et al. 1997). This would explain the relatively extensive overlap in diet (this study) and foraging areas (Sapoznikow and Quintana 2003) as a result of both species feeding relatively close to the colony on abundant food resources. At times of food scarcity, resource overlap between Imperial Cormorants and Rock Shags may be reduced through a combination of differences in diving capabilities, maximum potential foraging ranges, and foraging behavior. Information on prey abundance and availability is needed to adequately interpret patterns of resource overlap among species (Wiens 1989).

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MOVEMENTS OF BLACK VULTURES BETWEEN COMMUNAL ROOSTS IN FLORIDA

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ABSTRACT.—Communal roosts are important resources for local populations of the Black Vulture (*Coragyps atratus*), but these roosts are increasingly becoming the focus for complaints of wildlife damage. We studied movements of Black Vultures between communal roosts in Florida using mark-resight methods. We marked 416 Black Vultures with patagial tags at two communal roosts in Orange County, Florida. A total of 1,245 resightings of 226 individuals were recorded over a 3-year period. Black Vultures made one-way movements between communal roosts of up to 152 km, and two-way movements (i.e., birds left a site and subsequently returned) between communal roosts of up to 144 km. Patterns of resightings indicated that some Black Vultures use several roosts over wide geographic ranges during parts of their lives. Long distance exchanges between roosts and high nightly turnover of membership at roosts leads to concerns that control of nuisance Black Vulture roosts has the potential to impact nontarget populations in a geographic area well beyond a given communal roost. *Received 1 May 2003, accepted 14 August 2003.*

Communal roosting in birds has attracted the attention of ornithologists for many decades, but no consensus on the origin or function of avian communal roosting behavior has been reached (e.g., Beauchamp 1999, Dall 2002). An interesting example is found in the Black Vulture (*Coragyps atratus*), which roosts year round at persistent communal roost sites (Buckley 1999). Individual Black Vultures appear to derive several benefits from communal roosting, including information exchange (Rabenold 1987a), facilitation of group foraging (Buckley 1996, Stolen 2000), opportunities for social interaction (Stolen 1996), and possible protection from predators (Buckley 1996).

Black Vulture communal roost use is complex, and individuals use communal roosts in different ways during different life stages. For example, nesting adults regularly use the roosts closest to their nest sites, while young adults that no longer receive assistance from their parents often travel more widely among roosts (Rabenold 1987b). Over shorter time spans, individuals do not always return to the communal roost they used the previous evening, and mean nightly turnover at communal roosts as high as 33% has been documented (Rabenold 1987b).

Rabenold (1983) coined the term "roost system" to describe the series of nearby communal roosts used by a local population of Black Vultures in a given area, and found evidence that adults exert control over the membership of communal roosts in the areas near their nesting locations (Rabenold 1986, 1987b). Because most previous research has focused on how individual Black Vultures use roosts within a limited area, little information exists on the movement patterns of Black Vultures between more distant communal roosts. Here we report multiple observations of long distance movements of Black Vultures between communal roosts in Florida. This behavior has not been well documented previously and its occurrence has important implications for the management of nuisance Black Vulture communal roosts.

STUDY AREA AND METHODS

We studied two Black Vulture communal roosts, 12.75 km apart, located near Kissimmee, Osceola County, Florida. The four counties surrounding these roosts were 52% farmland, with 75% of that used as rangeland for cattle (Florida Office of Agricultural Statistics unpubl. data). The island roost was located on a small island, approximately 20 ha, in Bay Lake (28° 25′ N, 81° 34′ W). Several bald cypress (*Taxodium distichum*) trees clustered near one end of the island were used as perches. Birds occasionally roosted in slash pines (*Pinus elliottii*) across the lake (approximately 500 m from the roost trees on the island). The

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conservation area roost was located along Bonnet Creek in a bald cypress and hardwood swamp (28° 19′ N, 81° 31′ W). The roost was several kilometers from paved roads or buildings in an area with limited public access. Roost trees were living bald cypress and several large, dead pines.

We captured Black Vultures at roosts with a walk-in trap that had a funnel-shaped entrance (Bloom 1987). Baiting was conducted for up to three days prior to trapping, and trapping was conducted from sunrise until 6 h after sunrise for up to three days (see Stolen 1996 for details). We marked Black Vultures using patagial wing tags following methods described in Young and Kochert (1987). Tags consisted of 3.5 × 18 cm colored vinyl streamers, secured to the left wing patagium using cattle ear tags of the same color and alphanumeric code. Different colors were assigned to the island and conservation area roosts (orange and green, respectively). Tags could be read from up to 150 m with a 45× spotting scope.

We conducted weekly surveys of the conservation area roost and monthly surveys of the island roost to count vultures and record the presence of tagged individuals. We also solicited information on sightings of tagged birds from local biologists, wildlife officers, and bird watchers using published requests for sightings in ornithological and government newsletters. We reviewed these sightings for accuracy and reliability before including them in analysis. We made opportunistic observations of tagged birds at numerous roosts and other locations throughout central and southwestern Florida. These sites ranged from 8–152 km from the study site roosts. The presence of interested observers at two of these roosts (Orlando Wetlands Park, Orange County, and the Richloam Fish Hatchery, Sumter County, both in Florida) resulted in numerous sightings from these locations.

RESULTS

We tagged 142 Black Vultures at the island roost during two trap sessions in 1990, and 274 Black Vultures at the conservation area roost during eight trap sessions between April 1991 and April 1992. We recorded 1,246 resightings of 226 individuals over a 3-year period ending in December 1993. The pattern of resightings at study site roosts showed that many of the birds remained in the area and used the study site roosts extensively. Of birds tagged at the island roost, 62% were resighted at least once; most of these birds were seen at the island roost only, although some individuals also were sighted at the conservation area roost or off the study area (Table 1). Of the birds tagged at the conservation area roost, 50% were resighted at least once. In contrast to the pattern at the island roost, the majority of these birds were seen at both roosts. Overall, 53.8% of all birds tagged were resighted at least once and 13.0% were seen at both roosts.

TABLE 1. Over half of 416 Black Vultures tagged during 1990 and 1991 at two communal roosts in central Florida were resighted. Resighting histories are summarized by locations where a bird was resighted (resighting category) and location tagged. Noteable is the large number of resightings at both roosts and off of the study site.

Resighting category	Location tagged[a]			
	Conservation area roost		Island roost	
	Proportion	Number	Proportion	Number
Tagging roost only	0.16	45	0.46	66
Both roosts	0.16	45	0.06	9
Other roost only	0.13	35	0.01	2
Off site only	0.04	11	0.08	11
Total resighted	0.50	136	0.62	88

[a] Total number of birds tagged: conservation area roost = 274, island roost = 142.

Forty-three tagged Black Vultures were resighted at 25 sites away from the study site, ranging 8–152 km from the tagging location, including 25 from among birds tagged at the island roost and 18 from among birds tagged at the conservation area roost (Fig. 1). Many of these distant sightings were made at communal roosts (Table 2). Ten of the tagged Black Vultures observed at a distant roost location were subsequently resighted on the study area, including five that were tagged at each roost. These birds were observed at five different distant roosts ranging from 58–144 km from the location of tagging (Fig. 1).

In addition to sightings of the birds we tagged, 24 Black Vultures tagged at other communal roosts in Florida by R. L. Thompson of the USDA Animal Control Office (R. L. Thompson pers. comm.) were observed at

FIG. 1. Locations of 57 distant sightings of tagged Black Vultures between 1990 and 1993. Numbers denote the location and the number of tagged birds sighted at each location. Letters show the locations of the five distant roosts at which tagged birds were sighted and subsequently returned to the study area: (a) Homosassa Springs State Park, 1 of 4 birds returned; (b) Richloam Fish Hatchery, 1 of 6 birds returned; (c) Vandenberg Airport, 1 of 2 birds returned; (d) Myakka River State Park, 1 of 3 birds returned; and (e) Orlando Wetlands park, 6 of 18 birds returned. The location of the study site is indicated by a solid square.

the study site roosts and at other locations in central Florida. Eleven of 142 birds tagged at a roost 10 km from the study site were resighted at a study site roost. Two Black Vultures tagged at a roost at Homosassa Springs State Park (Citrus County, Florida) 109 km distant were resighted on the study site (one at each roost). Six other Black Vultures tagged at Homosassa were resighted at the Richloam Fish Hatchery (Sumter County, Florida), which is 67 km distant. Three Black Vultures tagged at a roost at Lake Marian (Osceola County, Florida) 25 km distant, were resighted at study site roosts. One of the three Lake Marian birds also was sighted at the Richloam Fish Hatchery, 52 km from the study site roost and 64 km from the Lake Marian roost. Two other Black Vultures tagged at Lake Marian

TABLE 2. Thirty-eight sightings of Black Vultures tagged during 1990 and 1991 at two roosts in Orange County, Florida, were recorded at roosts at least 25 km distant. Ten of those individuals subsequently were resighted at the study site roost.

Resighting location	Sightings[a]	Distance to tagging roost (km)[b]	
		Island roost	Conservation area roost
Lake Marian, Osceola Co.	1 IR	25	—
Sewage Treatment Plant, Orange Co.	2 IR, 1 CAR	39	37
Orlando Wetlands Park, Orange Co.	8 IR, 10 CAR	59	58
Richloam Fish Hatchery, Sumter Co.	4 IR, 2 CAR	63	56
Vandenberg Airport, Tampa, Hillsborough Co.	1 IR, 1 CAR	90	92
Homosassa Springs State Park, Citrus Co.	4 IR	109	—
Wauberg Lake, Alachua Co.	2 IR	144	—
Myakka River State Park, Sarasota Co.	2 IR, 1 CAR	144	152

[a] IR = bird tagged at island roost; CAR = bird tagged at conservation area roost.
[b] Distance from the distant roost where sighted to the roost where the bird was tagged.

were resighted at the Richloam Fish Hatchery, and one was sighted at a location in Brevard County, 78 km from the tagging location.

DISCUSSION

Published information on the movement patterns of Black Vultures is limited. In Pennsylvania, Coleman and Fraser (1987) found that the mean distance traveled from communal roosts to feeding sites was 5.6 km (n = 270), and that 95% of daily flight distances were <15 km (Coleman and Fraser 1989). This suggests that Black Vultures may use communal roosts as the center of daily foraging activities. Our repeated sighting of many of the tagged Black Vultures at both study site roosts supports this idea. Other studies have documented long distance movements (170–1,152 km) of Black Vultures from locations where they were marked (Parmalee 1954, Parmalee and Parmalee 1967, Rabenold 1983, Sweeney and Fraser 1986). Because the majority of these distant sightings were made away from communal roosts, they do not shed much light on Black Vulture communal roosting behavior. One exception was reported by Sweeny and Fraser (1986), who observed a Black Vulture at a roost 190 km from where it was tagged.

A significant finding of our study was that Black Vultures routinely travel to distant communal roosts up to 152 km away. Our results also document that Black Vultures often return to a communal roost following visits to distant communal roosts. These movements, occurring at distances ranging 61–152 km from the original tagging locations, have not been well documented previously for the Black Vulture. Two lines of evidence indicate that Black Vultures in Florida routinely use distant communal roosts. First, birds tagged at both study site communal roosts demonstrated this behavior. Second, birds tagged at two other communal roosts in central Florida also were observed moving between distant roosts. Thus, movement of birds between local roost systems occurred in both directions. By documenting the extensive use of distant roost locations by tagged Black Vultures, our results suggest that local populations of Black Vultures may be connected to other more distant roosts systems.

Communal roosts often are identified at or in the vicinity of complaints of nuisance Black Vultures. Control recommendations often include alteration of the roost habitat, harassment of the birds as they enter the roost in the evening, or translocation or killing of the birds (Lowney 1999). Our results show that efforts to reduce the use of a single Black Vulture communal roost most likely will impact a much larger population of birds than are present at the roost at any given time. Until more is known about the dynamics of Black Vulture communal roost use, management techniques such as habitat modification and harassment for roost dispersal should be used with caution. Because of the high turnover rate of birds at individual roosts, relocation attempts or killing of individuals are not recommended for reducing the numbers of Black Vultures using roosts. We recommend instead that more research be conducted on Black Vulture movement patterns to develop useful management strategies for nuisance vulture roosts.

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AGE AND SEX DIFFERENCES IN THE TIMING OF SPRING MIGRATION OF HAWKS AND FALCONS

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ABSTRACT.—We trapped 994 hawks during spring migration in years between 1953 and 1972. We obtained sufficient numbers to comment on age or sex differences, or both, in the timing of migration of six species. Adults migrated earlier in most species, presumably because most adults but few juveniles breed. Adult male Sharp-shinned Hawks (*Accipiter striatus*) migrated significantly before adult females and the larger (presumably female) Red-tailed Hawks (*Buteo jamaicensis*) migrated significantly earlier than smaller individuals. Juvenile female Sharp-shinned Hawks and Cooper's Hawks (*A. cooperii*) migrated before males, probably because more juvenile females than males breed. *Received 14 January 2003, accepted 3 June 2003.*

Mueller et al. (2000) analyzed age and sex differences in the timing of fall migration of 10 species of hawks and falcons at Cedar Grove, Wisconsin. They found that adults migrated later than juveniles in eight species and that males migrated later than females in five of these. Mueller et al. (2000) hypothesized that prolonged occupancy of the territory during fall provided an advantage the following breeding season with the greatest advantage accruing to the sex that is the primary defender of the territory. Females migrated later than males in Cooper's Hawks (*Accipiter cooperii*) and Northern Goshawks (*A. gentilis*); females may be more attached to the breeding territory than males in these two species. Juveniles migrated later than adults in the Peregrine Falcon (*Falco peregrinus*), and there was no significant age difference in the timing of migration in the Rough-legged Hawk (*Buteo lagopus*). These two species breed in the Arctic where summers are short, adults must leave as soon as the young are independent, and adults may migrate more rapidly than juveniles.

The sex that is the primary defender of the territory would be expected to migrate earlier in spring than the other sex. Adults, which usually breed, would be expected to migrate earlier in spring than juveniles, which rarely breed in most species. It is difficult to determine the sex of most raptors in the field. Because of the sexual size dimorphism, trapping a migrant raptor permits the determination of sex in many species and an approximation of sex in others. We report here on spring migrants trapped at Cedar Grove, Wisconsin.

METHODS

We trapped 994 migrating hawks of 12 species at the Cedar Grove Ornithological Station (43° 33′ N, 87° 21′ W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin, on 414 days during 12 springs from 1953 to 1972. We obtained sufficient individuals to distinguish age differences in five species, sex differences in adults and juveniles in four species, and sex differences in the American Kestrel (*Falco sparverius*) where age determination was not possible. We determined sex by plumage in American Kestrels and adult Northern Harriers (*Circus cyaneus*), and by measurement in Cooper's Hawks, Sharp-shinned Hawks (*A. striatus*), and juvenile Northern Harriers. Red-tailed Hawks (*Buteo jamaicensis*) could not be sexed but an estimate of sex was obtained by dividing the size distribution of wing chord into large and small individuals. This was not attempted in Red-shouldered Hawks (*B. lineatus*) because of small sample size.

We used the Mann-Whitney *U*-test to compare the timing of migration for age and sex groups. Statistics were performed in SYSTAT (Wilkinson 1989) on a Macintosh computer.

RESULTS

Adults migrated significantly earlier in spring than juveniles in the Northern Harrier, Cooper's Hawk, and Red-tailed Hawk, and in

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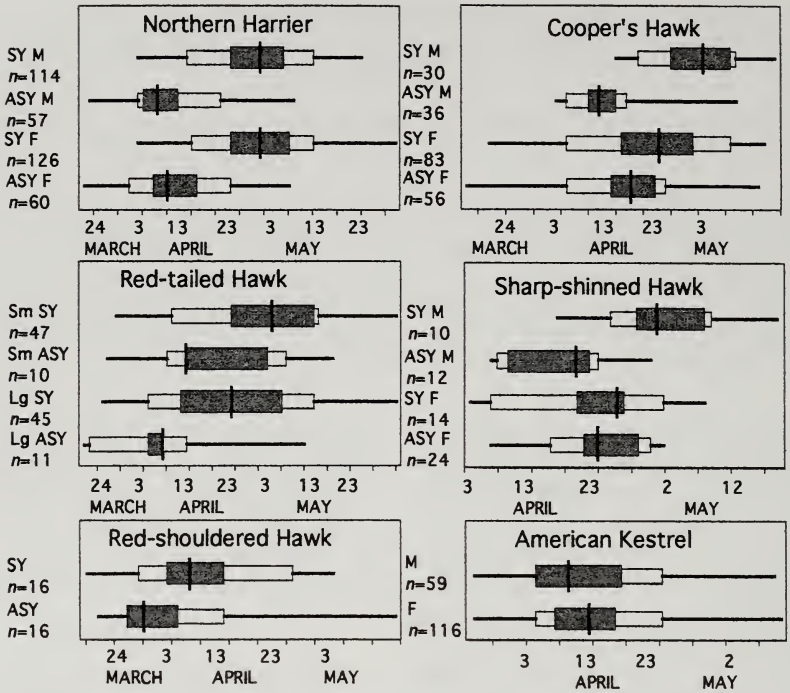

FIG. 1. Temporal distribution of hawks and falcons during spring migration along the western shore of Lake Michigan, 1953–1972. SY M are second year males (males in juvenal plumage); ASY M are after second year males (males in adult plumage); F are females; Sm (small) are Red-tailed Hawks with wing chords shorter than the mean, and thus presumably male; Lg (large) are Red-tailed Hawks with wing chords longer than the mean, and thus presumably female. The vertical lines indicate medians, and the shaded bars, white bars, and horizontal lines enclose the median, 33%, 67%, and 95% of the sample distributions.

male Sharp-shinned Hawks (Fig. 1, Table 1). There was no significant age difference in the timing of migration in Red-shouldered Hawks and female Sharp-shinned Hawks. For adults, males migrated significantly earlier in Sharp-shinned Hawks, and large individuals (presumably females) migrated significantly earlier in the Red-tailed Hawk. For juveniles, females migrated significantly earlier than males in the Cooper's Hawk and the Sharp-shinned Hawk. No other age or sex differences were statistically significant.

DISCUSSION

Adults migrated before juveniles in five species for which age could be determined, although the difference was not statistically significant in Red-shouldered Hawks and female Sharp-shinned Hawks. In most species of raptors, second year birds usually do not breed. Up to 23% of breeding female Northern Harriers are juveniles, but only 5–8% of the males are (MacWhirter and Bildstein 1996). In Cooper's Hawks, 6–22% of breeding females are juveniles, but juvenile males apparently breed only rarely (Rosenfield and Bielefeldt 1993). Some juvenile Sharp-shinned Hawks breed, mostly females, but most do not until they are older (Bildstein and Meyer 2000). Few juvenile Red-tailed Hawks breed (Preston and Beane 1993). Usually only adults breed in the Red-shouldered Hawk, but juveniles (mostly females) have been reported breeding with adults (Crocoll 1994). American Kestrels, however, typically breed in their second year (Bird 1988). Thus, individuals that are likely to breed migrate earlier in spring than those that are unlikely to breed. Adults migrated significantly later than juveniles during fall in all five of these species (Mueller et al. 2000), suggesting that breeders are more attached to the home area than nonbreeders.

In adults, males migrated earlier in four of

TABLE 1. Age and sex differences in the timing of spring migration along the western shore of Lake Michigan, 1953–1972. ASY birds migrated later than SY birds in most species. Statistical results are from Mann-Whitney tests.

Species	Comparison[a]	Sample sizes	*U*	*P*
Northern Harrier	SY M versus ASY M	114, 57	997	0.001
	SY F versus ASY F	126, 60	1,304	0.001
	ASY M versus ASY F	57, 60	1,522	0.305
	SY M versus SY F	114, 126	6,955	0.672
Cooper's Hawk	SY M versus ASY M	30, 36	112	0.001
	SY F versus ASY F	83, 56	1,787	0.012
	ASY M versus ASY F	36, 56	837	0.106
	SY M versus SY F	30, 83	1,670	0.004
Sharp-shinned Hawk	SY M versus ASY M	10, 12	10	0.001
	SY F versus ASY F	14, 24	174	0.855
	ASY M versus ASY F	12, 24	205	0.042
	SY M versus SY F	10, 14	30	0.019
Red-tailed Hawk	ASY versus SY	21, 92	1,431	0.002
	Sm ASY versus Lg ASY	10, 11	86	0.028
	Sm SY versus Lg SY	47, 45	1,239	0.156
Red-shouldered Hawk	SY versus ASY	17, 16	44	0.134
American Kestrel	M versus F	59, 116	3,282	0.656

[a] SY = Second year, i.e., birds hatched the previous year.
ASY = After second year, i.e., birds hatched prior to the previous year.
M = Males.
F = Females.
Sm = Birds with wing chords shorter than the mean.
Lg = Birds with wing chords longer than the mean.

the five species where samples were adequate, but the difference was statistically significant only in Sharp-shinned Hawks. In adult Red-tailed Hawks, larger (presumably female) birds migrated significantly earlier than smaller birds. Male Northern Harriers arrive on the breeding territory before females (MacWhirter and Bildstein 1996), and the same is true of the American Kestrel (Bird 1988) but information is lacking for the other four species. The sex that is the primary defender against conspecifics might be expected to migrate earlier, but there is little information available. Males are more active in territorial defense in the American Kestrel (Bird 1988) and Cooper's Hawk (Rosenfield and Bielefeld 1993). Both sexes defend the territory against members of their own sex in the Northern Harrier. There is no published information on the other species.

Males usually are the sex most attached to the territory and are more active in territorial defense than females (Newton 1979), and leaving the territory later in fall and returning earlier in spring would be an advantage. Males provide much of the food for the female and young during the breeding season, and prolonged familiarity with the territory might be advantageous in hunting. Adult males migrated significantly later than adult females during fall in four of the six species; the difference was almost significant ($P = 0.08$) in a fifth, the Northern Harrier; and females migrated later than males in the Cooper's Hawk. The hypothesis that the sex which is most attached to the territory migrates later in fall and earlier in spring thus fails to hold for two of the five species in this study where sex was determined. We cannot explain these differences between spring and fall in the timing of migration of the sexes.

For juveniles, females migrated earlier in three of the four species where this could be determined, but the difference was significant only in Cooper's and Sharp-shinned hawks. There was no significant difference in Red-tailed Hawks and no discernible difference in Northern Harriers. Juvenile females may migrate earlier than males because they are more likely to breed than juvenile males.

Juvenile males leave their natal areas significantly later in fall than females in 8 of 10 species (Mueller et al. 2000). Thus, we might expect juvenile males to migrate earlier in

spring than females, but the opposite was true. The Cooper's Hawk is one of two species in which adult females migrated significantly later than adult males during fall, and in this species juvenile males migrated significantly later than juvenile females during fall; the Northern Goshawk is the other species and there was no significant age (SY versus ASY) difference in the timing of migration of juveniles (Mueller et al. 2000). Females disperse farther than males in birds, both from their natal site and previous breeding site (Greenwood 1985). Natal philopatry has been studied adequately in only one species of raptor, the Eurasian Sparrowhawk (*A. nisus*), in which females dispersed farther than males (Newton 1979). Perhaps the longer residency in the breeding area during fall by juvenile males facilitates philopatry.

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LATITUDINAL VARIATION IN THE DEFINITIVE PREBASIC MOLT OF YELLOW WARBLERS

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ABSTRACT.—We compared the definitive prebasic molt schedules of Yellow Warblers (*Dendroica petechia*) at two northern temperate breeding sites: the Vermont Institute of Natural Science (Vermont) in Woodstock, Vermont, and North Point (James Bay) on the southwestern coast of James Bay, Ontario. The two sites are separated by 8° of latitude. Yellow Warblers initiated molt significantly earlier in Vermont than at James Bay, with respective mean onset dates of 29 June and 20 July, but durations and rates of molt did not differ significantly between populations at the two sites. Mean individual molt durations spanned 44.5 days in Vermont and 40.0 days at James Bay. Molt rate of females differed significantly between the two sites, but male rates were similar. Based on number of primaries growing simultaneously, Yellow Warblers in both Vermont and James Bay appear to undergo a rapid and intense molt. The earlier and slightly more protracted molt of Yellow Warblers in Vermont may result from their earlier spring arrival and longer breeding season. *Received 22 November 2002, accepted 11 March 2003.*

Migratory birds that breed in seasonally variable environments typically partition reproduction, molt, and migration within their annual cycles. Energy resource conflicts are minimized by the temporal segregation of such events (Kendeigh 1949, Farner 1964, Bancroft and Woolfenden 1982). At temperate and northern latitudes, energetic constraints may become heightened by a shortened breeding season and the costs of migration. Several migratory passerine species overlap breeding with the definitive prebasic molt (Haukioja 1971, Green and Summers 1975, Rimmer 1988, Jenni and Winkler 1994, Hemborg et al. 1998). Molt and migration overlap appears to be less common (King 1974; but see Dolink and Blyumenthal 1967, Newton 1968, Cherry 1985, Rimmer 1988, Hahn et al. 1992), presumably because of the conflicting energetic and aerodynamic demands of both activities.

Few published molt studies exist for discrete breeding populations of North American wood-warblers (Parulinae) from northern temperate latitudes. Particularly lacking are data on the precise scheduling of reproduction, molt, and migration of known-identity breeders (but see Rimmer 1988). Although differences in the timing of prebasic molt between latitudinally separated populations of other passerine groups have been reported (Mewaldt and King 1978, Mulvihill and Rimmer 1997, Heise and Rimmer 2000), there are no published data for any wood-warbler species. Yellow Warblers (*Dendroica petechia*) breeding at northern latitudes undergo a rapid, intense molt that regularly overlaps the end of nesting and the beginning of southward migration (Rimmer 1988). This molt regime appears to be dictated by a late spring arrival, coupled with deteriorating food supplies and the onset of early cold weather in late summer. In this paper, we compare data collected at a central Vermont breeding site with those previously published from the James Bay coast, in order to examine latitudinal variation in the prebasic molt schedules of adult Yellow Warblers.

STUDY AREA AND METHODS

We collected molt data during the summers of 1986–2000 at the Vermont Inst. of Natural Science (hereafter "Vermont") in Woodstock, Vermont (43° 36′ N, 72° 32′ W) and from 1980–1984 at North Point (hereafter "James Bay") on the southwestern coast of James Bay, Ontario (51° 29′ N, 80° 27′ W). The two sites are separated by a straight-line distance of 1,030 km. For descriptions of the James Bay site and data collection methods, see Rimmer (1988). We collected molt data in Vermont on a 3-ha site characterized by second growth deciduous shrub-woodland, consisting of brushy thickets interspersed with stands of mostly mature trees 10–20 m in height. Dominant canopy species included

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sugar maple (*Acer saccharum*), quaking aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*); dominant shrubs included willow (*Salix* spp.), autumn olive (*Elaeagnus umbellata*), steeplebush (*Spiraea communis*), and common buckthorn (*Rhamnus cathartica*). From 1986–2000, we operated 19–21 mist nets (12 × 2.6 m, 36-mm mesh) 1–3 days/week during July and 5 days/week from 1 August to early November. Nets were opened for 6 h/day, beginning 0.5 h before sunrise, except during adverse weather conditions.

We banded all captured individuals with USFWS aluminum leg bands. We aged Yellow Warblers as either second year (SY) or after second year (ASY), according to criteria in Pyle et al. (1997). When individuals did not fit clearly into either age category, they were designated as after hatching year (AHY). Males and females were distinguishable in all plumages and at all stages of molt.

We used a conventional molt scoring system (Ashmole 1962, Newton 1966) which assigns each remex and rectrix a score of 0 to 5 as follows: 0 = not dropped, 1 = missing or in pin, 2 = "brush" stage to one-third grown, 3 = one-third to two-thirds grown, 4 = two-thirds to full-grown but with waxy sheath remaining, 5 = completely regrown. We followed Bancroft and Woolfenden (1982) in obtaining a remigial score for all 18 primary feathers and both the left and right sixth secondary. This remigial score results in a more linear relationship of molt score to date than by using primary score alone (Bancroft and Woolfenden 1982). The assumption of linearity between molt score and date is important if recapture data and regression analysis are used to estimate rate and duration of molt (Newton 1966, Bancroft and Woolfenden 1982, Rimmer 1988). A remigial score of 0 indicates that remigial molt had not begun, while a score of 100 indicates completion of this molt.

We examined remigial molt on the assumption that its duration provides an accurate index of the period during which a bird's entire plumage is replaced (Bancroft and Woolfenden 1982, Rimmer 1988). We estimated the duration of prebasic molt, based on the rate of remex molt, in two ways: (1) using linear regression analysis of remigial scores versus date for all individuals in active remigial molt, and (2) from individuals captured two or more times in the same molt cycle with a minimum of five days between captures. However, regression analysis underestimates molt rate when molt onset is highly asynchronous within a population (Pimm 1976, Bancroft and Woolfenden 1982, Rimmer 1988). Due to the asynchronous onset of molt in Vermont birds, we used only recapture data in our statistical analyses, although we present regression results for comparative purposes.

In calculating individual molt rates, we used only first and last captures. For these individuals, we calculated rates of molt by dividing the difference in remigial score by the number of days between captures. Because rates of molt decrease late in the molt cycle of Yellow Warblers (Rimmer 1988), we used only birds whose initial remigial score was <85. Rate calculations are expressed as points/day. We calculated dates of molt onset for individuals and the sampled population by extrapolating rates from recaptured birds.

RESULTS

Sequence, rate, and duration of molt.—The sequence of remex and rectrix molt in Yellow Warblers in Vermont closely matched that of birds examined at James Bay (Rimmer 1988). The innermost primary invariably was the first flight feather to drop, and primaries were replaced in descending order, proximal to distal. The outermost secondary usually began molting simultaneously with primary 6 or 7, and secondaries 1–6 were replaced distal to proximal. Secondary 6 typically was the last remex to complete growth.

We calculated the remex molt rate of 13 Vermont individuals caught more than once during the same remigial molt cycle (Fig. 1). The mean molt rate of females did not differ significantly from that of males (Table 1; $t_{11} = 0.003$, $P = 0.99$). Small sample sizes of known-aged birds precluded age-related molt analyses (Table 1).

Vermont males ($n = 7$) completed remigial molt during a mean of 45 days ± 5.64 SD, females ($n = 6$) during 44 days ± 5.86 SD. Remex molt rates of males ranged from 1.61–3.00 points/day, while females molted at rates between 1.00 and 3.05 points/day. The greatest deviations from mean molt rates were ex-

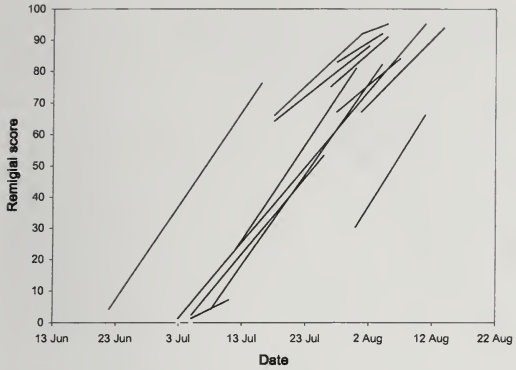

FIG. 1. Nearly parallel slopes of lines connecting remex scores of individual Yellow Warblers examined two or more times during the definitive prebasic molt in Vermont, 1986–2000, indicate that overall molt rates were similar among all birds.

hibited by individuals examined only early or late in the molt cycle or in which the interval between successive captures was short. Rates were slowest during the early and late stages of molt (Fig. 1), when fewer remiges were growing simultaneously. However, the similarity of mean molt rates between males and females and the nearly parallel slopes of the longest lines in Fig. 1 indicate that the overall molt rate was very similar among all Vermont birds, independent of initiation date.

For both male and female Yellow Warblers, molt rates did not differ significantly between Vermont and James Bay (females: $t^5 = 1.71$, $P = 0.14$; males: $t^9 = 0.63$, $P = 0.27$; Table 1). *Post hoc* power for different effect size (Johnson 1999) on differences in molt rates was 0.80 for females ($n = 19$) and 0.82 for males ($n = 17$), with an effect size of 1 for each. Molt durations reflected these small differences, with James Bay females completing molt in only 6 fewer days than Vermont females (44 versus 38 days), while James Bay males molted only 3 days more rapidly than Vermont birds (45 versus 42 days).

We evaluated the intensity of remigial molt by determining the maximum number of primaries growing simultaneously. This stage in the molt corresponded with remigial scores between 51 and 70. The mean number of simultaneously growing primaries during this period did not differ significantly between James Bay and Vermont Yellow Warblers (6.3 ± 0.85 SD and 5.2 ± 0.21 SD, respectively; $t^{12} = 1.85$, $P = 0.20$).

Chronology of molt.—We examined molting Yellow Warblers captured from late June to early September. The onset and termination of molt spanned 3-week periods between late June and mid-July and early to late August, respectively (Fig. 2). The mean molt onset date for all Yellow Warblers in Vermont was 29 June. Females began molting earlier than males, but the respective mean initiation dates of 27 June and 1 July did not differ significantly ($t^{11} = 0.75$, $P = 0.47$). The mean molt termination date for all Vermont birds was 12 August. Females completed molt on 10 August, 5 days earlier than the mean male termination date of 15 August. This difference also was not significant ($t^{11} = 1.28$, $P = 0.23$).

Overall, Yellow Warblers in Vermont began and ended prebasic molt 21 days earlier than the birds at James Bay (Table 2). Molt onset dates for Vermont males were significantly earlier than for James Bay birds ($t^{15} = 4.08$, $P = 0.001$), and Vermont females initiated molt significantly earlier than did females at James Bay ($t^{18} = 8.53$, $P < 0.0001$). Mean molt termination dates of Vermont males and females also were significantly earlier than those of James Bay birds (males: $t^{13} = 4.14$, $P = 0.001$; females: $t^{18} = 4.79$, $P = 0.0001$).

TABLE 1. Male and female Yellow Warbler molt rates from Vermont (VT) and James Bay, Ontario (JB), based on recapture data and linear regression.

	Recapture			Regression		
Class	*n*	Rate[a]	SD	*n*	Rate[a]	SD
Males-VT	7	2.142	0.657	44	1.831	0.191
Males-JB	10	2.313	0.368	94	2.178	0.093
Females-VT	6	2.140	0.821	31	2.191	0.365
Females-JB	13	2.704	0.260	123	2.384	0.097

[a] Change in remex score per day (see Methods).

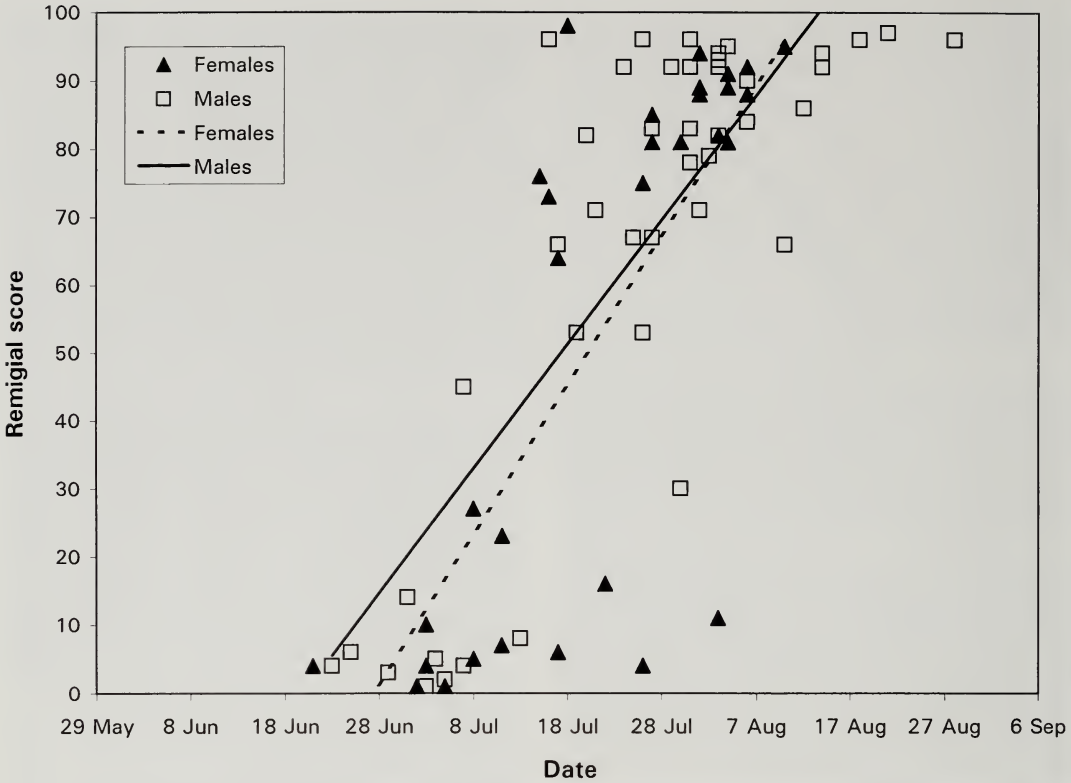

FIG. 2. Remex scores of Yellow Warblers examined during the definitive prebasic molt in Vermont, 1986–2000, show that onset and termination dates spanned 3-week periods between late June and mid-July and early to late August, respectively.

Molt and migration.—Although we could not reliably distinguish between local and transient birds in our mist net samples, we examined the integration of molt and migration under the assumption that most unbanded Yellow Warblers captured after 15 July were nonlocal birds (Laughlin and Kibbe 1985). The dates of capture for unbanded adults and immatures after 15 July were similar; mean capture date for adults (n = 30) was 6 August ± 16.5 days, mean capture date for immatures (n = 66) was 4 August ± 14.2 days. We recaptured four adults examined both in early or mid-molt and in nearly complete basic plumage, indicating that these individuals had completed remigial molt at our study site.

DISCUSSION

Yellow Warblers in Vermont required a mean of 44.5 days to complete remigial molt, 4.5 days longer than the mean molt duration (40.0 days) at North Point. Typically, migratory passerines breeding at northern temperate latitudes undergo a more rapid molt than sympatric, nonmigratory populations and species, or those breeding farther south (Dolnik and Blyumenthal 1967, Evans et al. 1967, Morton et al. 1969, Haukioja 1971, Mewaldt and King 1978). The molt durations of Yellow Warblers are considerably shorter than those reported for two other temperate wood-warbler species (Foster 1967, Nolan 1978), although precise data of individuals are lacking in those studies. Black-and-white Warblers (*Mniotilta varia*) breeding at two widely separated latitudes (New England and James Bay) showed similar mean durations of 45 days in both areas (T. Lloyd-Evans and CCR unpubl. data). Because few comparable molt data exist among the Parulidae, however, there is little basis for evaluating the prebasic molt patterns of Vermont Yellow Warblers with respect to other members of this family.

Yellow Warblers breeding in Vermont begin

TABLE 2. Estimated molt onset and termination dates for recaptured Yellow Warblers from Vermont (VT) and James Bay, Ontario (JB).

		Molt onset		Molt termination	
Class	*n*	Date	SD[a]	Date	SD[a]
Males-VT	7	1 July	±10.0	15 August	±5.9
Males-JB	10	17 July	±6.7	28 August	±7.7
Females-VINS	6	27 June	±7.5	10 August	±9.1
Females-JB	13	22 July	±5.3	28 August	±7.7
All Birds-VT	13	29 June	±8.7	12 August	±7.7
All Birds-JB	23	20 July	±6.3	28 August	±7.2

[a] Number of days.

and finish the remigial molt 2–3 weeks earlier than birds at northern latitudes. Both males and females exhibited this pattern. There are approximately 8° of latitude between Vermont and North Point, corresponding to a delay in molt onset of 1.8–2.6 days/degree northward. This difference is higher than the 0.4–1.0 days/degree for Chaffinches (*Fringilla coelebs*; Noskov 1975), but is similar to that reported for White-crowned Sparrows (*Zonotrichia leucophrys*, 2.6 days/degree; Mewaldt and King 1978). Both male and female Black-and-white Warblers in New England molted 13–14 days earlier than the same sex at North Point, presumably reflecting an earlier spring arrival and an earlier breeding season in the south (T. Lloyd-Evans and CCR unpubl. data). The mean known fledging date of five Yellow Warbler nests at Woodstock was 21 June (CCR unpubl. data), three weeks earlier than the mean fledging date of 11–12 July at North Point (Rimmer 1988). Thus, the earlier breeding chronology of the southern population appears to dictate, at least in part, its earlier molt schedule.

Passerine molt studies at northern temperate latitudes have shown that males tend to begin molting earlier than females (Mewaldt and King 1978, Tianen 1981, Rimmer 1988). Other studies at lower latitudes have found no significant sexual differences in molt onset (Newton 1966, Snow 1969, Nolan 1978, Heise and Rimmer 2000). Yellow Warblers appear to follow this pattern, as James Bay males initiate molt significantly earlier (5–7 days) than females (Rimmer 1988), but both sexes initiate molt on similar dates in Vermont. Rimmer (1988) suggested that a delayed molt onset in North Point females might result from their physiological inability to initiate molt as early as males, due to more pronounced energetic constraints caused by nest construction, egg synthesis, incubation, brooding, and nestling feeding duties during a relatively short summer. The earlier and more protracted breeding season of Vermont females may impose fewer such constraints and enable their relatively earlier initiation of molt.

While both sexes of Yellow Warblers in northern Ontario molted more rapidly than respective Vermont birds, differences were slight. The lack of significant geographic difference in molt rates may have resulted from low statistical power associated with small sample sizes and small effects. The result is particularly surprising for females, given likely differences in ecological and physiological constraints facing birds at the two localities. A relatively more rapid molt in James Bay females might be expected in order to compensate for their delayed start in the face of selective pressures to migrate as early as possible due to diminishing late summer insect food resources. The lower rate of molt of James Bay males relative to James Bay females may have resulted in part from the males' earlier onset, enabling them to avoid the costs of a rapid molt, and from the males' relatively higher energy expenditure during molt, since many continued to sing and apparently maintained territories until their southward departure (Rimmer 1988).

Despite a latitudinal difference of 8° between James Bay and Vermont, Yellow Warblers at the northern site molted only 4.5 days faster than their southern counterparts. This difference seems surprisingly small if ecological constraints at the two sites are driving respective molt schedules. A more protracted

molt would seem to be the optimal pattern for a bird facing relatively fewer constraints on its time and energy, as has been shown in sedentary passerines at high elevations (Pitelka 1958, Newton 1966, Orell and Ojanen 1980; Common Redpolls, *Carduelis flammea*, at James Bay, CCR unpubl. data), wintering Palearctic warblers (Pearson 1973, Price 1981), and resident versus migrant shorebird populations (Pienkowski et al. 1976). With an earlier, more prolonged breeding season and a more extended period of arthropod prey abundance in Vermont (CCR unpubl. data), Vermont Yellow Warblers might be expected to undergo a less rapid and intense molt than the 44.5 days we documented. However, individual Vermont birds, particularly females that we examined during the peak of the remigial molt, showed wing gaps nearly as large as those of North Point birds, and they may have been similarly incapable of sustained flight (Rimmer 1988). This suggests that both populations experience strong selective pressure to compress their prebasic molt. The energetic costs of a rapid molt, such as decreased thermoregulatory abilities and reduced flight efficiency, combined with the need to prepare physiologically for the impending long-distance migration, may impose an upper limit on the molt rate of James Bay Yellow Warblers and prevent further acceleration.

It is unclear from our data whether or not adult Yellow Warblers in Vermont regularly migrated before completing their prebasic molt. Based on four recaptured individuals examined at the beginning and end of molt, we believe that Vermont birds complete remigial molt on the breeding grounds. Although many Yellow Warblers appear to depart Vermont in late July (Laughlin and Kibbe 1985), well before the mean molt termination date of Vermont birds, several studies have documented that breeding area departures do not necessarily indicate migration onset (Nolan 1978, Rimmer 1988, Rappole and Ballard 1987, Vega Rivera et al. 1998). At James Bay, most male Yellow Warblers remained on breeding territories throughout the summer and departed during the late stages of remigial molt, while females showed comparatively little postbreeding site attachment and appeared to undergo a molt dispersal (Rimmer 1988).

Throughout their eastern North American breeding range, Yellow Warblers are among the earliest wood-warblers to undergo fall migration (Laughlin and Kibbe 1985, Veit and Petersen 1993, Bull 1998, Lowther et al. 1999); southern populations appear to depart earlier than those in the north (Lowther et al. 1999). Arrivals on Mexican wintering grounds begin in late July, mid- to late August in southern Central America (Lowther et al. 1999). Yellow Warblers are strongly territorial during winter, particularly toward members of other small, insectivorous species, suggesting that intense interspecific competition for rich arthropod food resources occurs (Greenberg and Salgado-Ortiz 1994). Under the assumption that high quality winter habitats are limiting for many species of long-distance migrants and that occupancy of optimal winter habitats enhances overall fitness (Marra et al. 1998), early-arriving Yellow Warblers may gain an important selective advantage. Both intra- and interspecific habitat competition may be involved if Yellow Warblers from different breeding localities are in contact on the wintering grounds, as has been shown for other species (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 2001). Selection for early arrival on the wintering grounds has been suggested for several species of *Sylvia* warblers breeding in Europe (Fransson 1995, Hall and Fransson 2001). For birds breeding at more southern latitudes such as Vermont, the aerodynamic and energetic costs of a rapid molt may be outweighed by the benefits of a relatively early southward departure and winter arrival. Northern populations such as those at James Bay may be unable to further advance or accelerate their molt, due to the ecological constraints of a high-latitude summer (Jenni and Winkler 1994, Hemborg et al. 1998). We believe that the unexpected compression of prebasic molt in Vermont Yellow Warblers may be an adaptive response more to resource competition on the wintering grounds, mediated through fall migration schedules, than to latitudinal and ecological differences between Vermont and James Bay.

The apparent selective pressures for a rapid molt in Yellow Warblers beg the question of why this and most other Nearctic-Neotropical migrant passerines have not evolved the seasonally divided molt strategies typical of

many long-distance Palearctic migrants (Alerstam and Högstedt 1982, Jenni and Winkler 1994, Holmgren and Hedenström 1995). By suspending prebasic molt, or postponing it entirely until arrival on their wintering grounds, Yellow Warblers theoretically could minimize their energetic costs while maximizing the benefits of early arrival on the wintering grounds. One possible explanation is simply that molt patterns are phylogenetically constrained, thus limiting the scope of adaptive responses. Conversely, arrival on the wintering grounds with a new set of high quality feathers might enhance survival (Holmgren and Hedenström 1995) through competitive advantages in territory acquisition and maintenance, thus promoting an earlier and/or more rapid postbreeding molt. Few empirical data exist to test such hypotheses in Yellow Warblers or other migrant passerines. A comprehensive review of passerine molt patterns across phylogenetic lines and life history strategies is needed to better elucidate the evolutionary mechanisms that shape the integration of molt into avian annual cycles (but see Svensson and Hedenström 1999).

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Notes on the Breeding Behavior of a Philippine Eagle Pair at Mount Sinaka, Central Mindanao

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ABSTRACT.—We documented the breeding behavior and diet of a Philippine Eagle (*Pithecophaga jefferyi*) pair from July 1999 to January 2000 in an isolated forest in Central Mindanao. We observed eight distinct courtship displays and several activity patterns on the nest. Copulation started two months prior to egg laying and continued until the first month of incubation, with a mean of 1.5 copulations per day. Seventy-four percent of the time devoted to incubation was by the female. The incubation period lasted 58 days. Throughout the incubation and early brooding phases the male provided food for the female and the young. Diet consisted of 17 prey items of four vertebrate taxa, mostly mammals, with civet cats (Family Viverridae) and flying lemur (*Cynocephalus volans*) representing the bulk of the diet. *Received 30 November 2001, accepted 15 August 2003.*

The Philippine Eagle (*Pithecophaga jefferyi*) is one of the most critically endangered birds of prey (Bildstein et al. 1998). It is endemic to the islands of Luzon, Leyte, Samar, and Mindanao of the Philippines. On Mindanao, eagles begin nesting from September to December in habitats ranging from primary lowland forests to highly disturbed woodlands. Recently, efforts were renewed to study the ecology and biology of this highly endangered raptor in an effort to devise management strategies for the long term conservation of the remaining population. An analysis of the eagles' nesting density suggest that there are about 200 pairs in Mindanao, with each breeding pair occupying about 133 km^2 (Bueser et al. 2003).

A complete breeding cycle in this species lasts two years, and successful pairs produce a single offspring (Gonzales 1968, Kennedy 1985). Since the detailed work by Kennedy (1977, 1985) on Philippine Eagle nesting biology, there have been few studies on the behavior and ecology of this species. Recently, new information on the eagles' breeding success (Miranda et al. 2000) and nesting density and population estimates for Mindanao Island (Bueser et al. 2003) have been published. This study describes the prey as well as the behavior of a pair of Philippine Eagles nesting in a relict forest in Central Mindanao, Philippines. This initial attempt to quantify activity patterns of a pair in an isolated forest habitat is relevant in the light of continued forest fragmentation in the Philippines, where the behavioral responses of Philippine Eagles to a shrinking habitat remain unknown.

METHODS

We gathered 703 h of behavioral data between July 1999 and January 2000 in Mount Sinaka, Cotabato Province, Philippines. Mount Sinaka (07° 20′ N, 125° 12′ E) is located in an isolated mountain range (peak at 1,448 m) with 19 km^2 of relict tropical forest. A nest was found in 1995, and was used during two successful nesting attempts. On 15 June 1999, the female was caught by a farmer and brought to the Philippine Eagle Foundation for rehabilitation. After one week the eagle's right wing was marked by clipping following Young and Kochert (1987), a radio transmitter was installed, and the bird was released the following week. The following month we located the female building a nest

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in a tree 200 m away from the old nest. The new nest was in a 29-m White Lauan (*Shorea contorta*, Dipterocarpaceae) tree at 750 m elevation, in an agroforest located on the mountain's western slope. We documented aerial displays and nesting behavior from several blinds located 40–150 m from the nest using 8 × 40 binoculars and a 20–56× spotting scope. We distinguished the female by her wing and by radio tracking. We directly observed and identified prey items delivered to the nest. The egg was laid on 16 November 1999 and hatched after 58 days of incubation. However, the chick died nine days later after three days of stormy weather.

RESULTS AND DISCUSSION

We recorded 118 h of notes on aerial displays, 293 h during nest building and before egg laying, and 292 h during incubation and brooding. We documented courtship behaviors during flight and on the nest. We distinguished four behaviors associated with aerial displays: mutual soaring, dive chase, talon presentation, and territorial flights. Mutual soaring was a circular gliding flight by both birds on thermals with the male usually soaring higher. Dive chases involved a diagonal drop in flight altitude, wings half folded toward the body, with the male trailing in pursuit. A dive chase sometimes was followed by a male talon presentation, which is characterized by a quick extension of the tarsi toward the back of the gliding female. On two occasions the female flipped over and quickly presented her talons. Such mutual talon presentation is known in many species of raptors (Brown and Amadon 1969). Mutual territorial flight behaviors were gliding flights with the male slightly above the leading female. Male courtship acts on the nest included vigorous calling toward the female in a low, horizontal posture (precopulation display), and delivery of prey for the female to consume (courtship feeding; Hatchwell et al. 1999). Food solicitation by the female, a pattern similar to the sexual solicitation display, also was observed. We also noted reciprocal pecking and preening actions directed toward the bill, wings, and other parts of the body of the other bird (allopreening).

We first observed delivery of nest materials on 17 September 1999, and deliveries continued throughout the study. The male brought more nest materials (n = 29 deliveries) than the female (n = 22 deliveries) prior to egg laying; the female made more deliveries (n = 33) than the male (n = 7) during brooding and incubation stages. Nest materials were delivered by both birds 1.7 times/day prior to egg laying, 1.2 times/day during incubation, and 3.0 times/day during brooding. The behavior sequence for nest building was as follows: the bird acquired leafy twigs (fresh or not) or a dried branch, deposited the material around the nest, pressed the materials with the breast, followed slowly by brooding. The mean duration of nest building behavior at the nest (excluding acquisition of materials) prior to egg laying was 5.7 min/day ± 4.2 SD (n = 43).

Copulation occurred on the nest and nearby perches, with or without prior courtship feeding. When prey was delivered to the unattended nest, the male issued loud and prolonged calls that changed into short, high-pitched whines when the female alighted on the nest. Calls became vigorous and gained speed while the male mounted, but gradually waned after copulation. When the male displayed precopulatory behavior without food, he did so in an apparently more submissive and wary manner, walking in a low horizontal posture toward the female and mounting her if she did not exhibit any rejecting behavior (e.g., an erect or threat posture). We observed 27 copulation attempts (25 during courtship, 2 during incubation), for a mean of 1.7 copulations/day between September and December 1999. The duration of copulation from mounting until dismounting lasted a mean of 19 s ± 3 SD (n = 6). In three instances, copulation occurred twice within a period of 30 min, and the maximum number of copulations observed in one day was three. Such copulation rates, which appear more than necessary for fertilization, has been reported in many raptor species (Newton 1979, Pandolfi et al. 1998, Arroyo 1999). Aside from ensuring successful fertilization, frequent copulation also is interpreted as a mechanism to strengthen the pair bond (Newton 1979).

The female performed 74% of the incubation duty (data from 963 instantaneous samples collected at 10-min intervals), but male incubation bouts were longer (the total time

that an adult spent on the nest bowl, sitting or not; male: mean = 3.1 h ± 1.7 SD, n = 11 bouts; female: mean = 1.4 h ± 0.8 SD, n = 70 bouts). Preening, defecation, or nest building by an attending adult commonly ended a bout of incubation. Unlike defecation, which was done only from a different tree, preening was performed also on the nest. When inside the nest bowl, an adult approached the egg with a distinctive gait: flexed toes with claws directed inward and feet leaning sideways. Before the adult sat, the egg was turned by reaching down 2–5 cm ahead of the egg then gently arching its bill toward the belly. While incubating, the adult tugged intermittently at the substrate in front of the egg. The mean time spent away from the nest was 21.0 h ± 3.8 SD (n = 5) for the male and 4.6 h ± 1.7 SD (n = 8) for the female. Turnover of incubation was signaled by calling or by alighting on the nest. The longest period that the egg was left unattended was 102 min. The male performed nighttime incubation on only three occasions, while the female incubated the egg during the rest of the nights throughout the duration of the incubation period.

We did not directly observe hatching, but surmised its occurrence from the behavior of the brooding female. On the morning of 13 January 1999, the female increased her tugging behavior and appeared to be sitting less tightly on the egg. The female turned the egg several times and nibbled frequently at the nesting materials. A few minutes after the chick hatched, the female moved the shell and ate a few pieces. No vocalizations were heard during hatching, but the adults exchanged calls about 3 h after hatching. The first parent-chick interaction consisted of light pecks and brushes by the female soon after the chick was able to raise its head.

Only the female brooded the chick and she spent less time brooding (62% of instantaneous samples, n = 321) than incubating (74% of 963 samples). Mean duration of female brooding bouts was 80 min ± 46 SD (n = 14). Although the male did not brood, he attended the nest for a mean duration of 6.7 min ± 9.7 SD (n = 9) when the female was away. The male was absent during the last three days of observation. The chick was left unattended for a maximum period of 232 min on 20 January 2000, eight days into the nestling stage (mean duration = 55.2 min ± 64.6 SD, n = 13). The female alone fed the chick; mean duration of feeding bouts was 13.0 min ± 6.6 SD (n = 11). The first meal was delivered on 15 January 2000, two days after hatching, and consisted of 36 pea-sized bits of rat meat. The chick was fed three times on the third day, three times on the seventh day, and twice on the ninth day.

The male eagle delivered 17 vertebrate prey items to the nest from October 1999 to January 2000: 11 during the courtship period (mean = 0.34 prey/day), 2 during incubation (mean = 0.10 prey/day), and 3 during brooding (mean = 0.50 prey/day). Of the 17 prey items, 16 (94%) were mammals. Prey items included flying lemurs (*Cynocephalus volans*, n = 7), civet cats (Family Viverridae, n = 7), rice field rats (*Rattus* spp., n = 2), and Philippine cobra (*Naja naja*, n = 1). Some of the prey items observed in this study also were reported by Kennedy (1985). Contrary to persistent reports by local people, no domestic animals were recorded.

Except for the Philippine cobra, all prey items were mostly gutted and decapitated, with portions of the fur already plucked off. Only the hindquarters of the civet cats were delivered to the nest. All prey appeared fresh, and probably came from new kills. Most of the delivered carcass was consumed, including the tail, bones, nails, and a few internal organs (e.g., kidney, intestine). Portions of prey not eaten immediately were left on the sides of the nest and in most cases were consumed later. On three occasions old prey remains that had not been consumed were removed from the nest. Unlike observations of Harpy Eagles (*Harpia harpyja*) in South and Central America (Alvarez-Cordero 1996, Galetti and de Carvalho 2000), we rarely observed discarded skeletal bones of prey. Although the sample size of prey was small, our observations suggest that studies of the diet of tropical birds of prey such as the Philippine Eagle based solely on prey remains rather than direct observations could underestimate prey species diversity.

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Adoption in the Red-cockaded Woodpecker

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ABSTRACT.—We observed a young male Red-cockaded Woodpecker (*Picoides borealis*) about 35 days old being fed by adults associated with a neighboring territory. A survey of biologists studying this species revealed similar acts of adoption had been observed elsewhere, but the behavior appeared to be very rare. Adoption generally implies a cost to adults because care is provided to unrelated young, but the situation is complicated in cooperative breeders such as the Red-cockaded Woodpecker. Adopted birds can help breeding adults raise additional young, and the adopted male we observed remained as a helper in its adopted territory and fed young the following breeding season. *Received 4 December 2002, accepted 12 March 2003.*

Acts of adoption (parental care of presumably unrelated offspring) have been recorded in <150 species of birds (Evans 1980, Riedman 1982). The behavior occurs with some regularity among species that nest colonially in high densities (Evans 1980), but it also has

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been reported in species that maintain larger breeding territories, particularly in association with loss of an adult breeder (Rohwer 1986). Despite its known occurrence among many species, new records of adoption can be noteworthy because they may help elucidate social and reproductive features associated with the behavior (Riedman 1982, Rohwer 1986). In this note we provide the first reports of probable acts of adoption in the Red-cockaded Woodpecker (*Picoides borealis*).

The Red-cockaded Woodpecker is an endangered species (Lennartz and Henry 1985) with a social breeding system (Lennartz et al. 1987, Walters 1990). This species has been the subject of extensive research throughout much of its range (Jackson 1995), but there have been no previous reports of adoption. The information we present stems from field observations in the Red Hills region (84° 18′ N, 30° 42′ W) of southwestern Georgia (Engstrom and Baker 1995) and a survey of biologists studying this species elsewhere in the southeastern U.S.

We uniquely banded many nestling and adult Red-cockaded Woodpeckers in the Red Hills to monitor the potential effects of translocation (U.S. Fish and Wildlife Service 2000). We banded three nestlings at approximately 6 days of age in May 2001 in territory A. In early June, we observed two of these banded birds (fledglings) in territory A and determined they were males (Jackson 1979). Within an hour of this observation, we observed the third bird banded in territory A (also a male) being fed by an adult in a neighboring territory (territory B). Another fledgling, which we had banded in the nest cavity at territory B, also was observed nearby. We found the adopted fledgling from territory A in territory B on later visits, but none of the fledglings banded in the nest of territory B were observed again.

Adults associated with the two territories were not uniquely banded, so we were not certain that the fledgling from territory A was the only bird that moved into territory B. However, the number of adults associated with each territory was estimated early in the breeding season, and this number had not changed at the time these observations were made (four adults in territory A, three adults in territory B). It is uncommon for new adults to be accepted quickly by territorial groups (Ligon 1970, Lennartz et al. 1987).

There were other factors that likely contributed to this event. First, the adopted bird was the smallest nestling banded in territory A (29 g compared to 31 and 33 g for the other nestlings). Birds with lower nestling weights are more likely to disperse in response to competition with siblings (Pasinelli and Walters 2002). Second, the distance between territory centers was only 850 m, but a small creek lined with hardwoods (i.e., unsuitable habitat) lay between the territories and may have inhibited return of the dispersing fledgling once it ventured into territory B. Third, and perhaps most important, the adopted bird from territory A was 5–6 days older than the birds banded in territory B. The adopted bird therefore likely was at an advantage in terms of its ability to follow foraging adults and beg for food (Ligon 1970).

We circulated a description of this event to 26 biologists working with woodpeckers elsewhere and asked if any had noted similar behaviors. C. A. Hess (pers. comm.) reported an act of adoption in the Apalachicola National Forest in northern Florida, also during 2001. A banded juvenile moved to an adjacent cluster and was observed being fed by adults from the adopted territory. In this instance, a nesting attempt by the adopting adults failed, so there were no resident fledglings. This event also involved a potential hardwood barrier between territories. J. A. Jackson (pers. comm.) reported observing adoption in populations in Mississippi and South Carolina several years ago. These cases had similarities to the incident we observed, including the thin strand of hardwoods separating clusters and dominance of the adopted bird as a result of hatching asynchrony. J. R. Walters (pers. comm.) reported instances where young birds moved into neighboring territories soon after obtaining independence, but switches by dependent fledglings were very rare; the latter behavior usually was associated with loss of an adult, so the fledgling that moved was not being fed as frequently. As noted, the number of breeding adults did not appear to change during our observations; however, we believe competition with dominant siblings in territory A contributed to the movement of the adopted bird out of its natal territory.

Adoption implies a cost to adult birds because time and energy are spent caring for presumably unrelated individuals (Rohwer 1986, Plissner and Gowaty 1988). There have been refinements to theories concerning the costs and benefits of adoption (Rohwer 1986), but the case of cooperative breeders presents a situation where benefits may accrue for adults that adopt. Young male Red-cockaded Woodpeckers often remain in their natal territories and help raise subsequent broods. Territories with helpers produce more offspring and are more stable than territories lacking helpers (Walters 1990). Helpers also reduce the number of feeding trips that adult breeders make during the nesting period (Khan 1999). These potential benefits were realized in this instance because the adopted male remained in territory B the following year and helped produce three fledgling females. The bird was still in the adopted territory on 1 October 2002 and may have helped produce additional progeny.

Although there are potential benefits associated with adoption, the behavior is rare in Red-cockaded Woodpeckers. Several biologists responding to our query reported observing fledglings in adjacent territories, but most of these were ignored by resident adults. Data from an old growth pine forest (Engstrom and Sanders 1997), which presumably resembles pre-Columbian conditions, suggest woodpecker territories were more tightly aggregated historically. Occasional movements of young among territories could have been more likely under these conditions. Why certain groups adopt wandering fledglings while others ignore these individuals probably is linked to special circumstances that defy generalizations. In addition to some of the circumstances mentioned above (e.g., fledgling interactions, asynchronous hatching, habitat barrier, number of adults, and loss of young), sex-based plumage differences evident in young Red-cockaded Woodpeckers (Hooper et al. 1980, Jackson 1979) would make it easy for adults also to consider the sex of wandering fledglings prior to adoption.

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Intergroup Infanticide in Cooperatively Polyandrous White-winged Trumpeters (*Psophia leucoptera*)

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ABSTRACT.—I observed a population of White-winged Trumpeters (*Psophia leucoptera*) in undisturbed lowland moist forest in Peru. During 2,460 h of focal observations, I observed one instance of infanticide that occurred when a permanent group killed the 7-day-old chick of an intruding group that was using a portion of its territory. Trumpeter groups defend large, year round, contiguous territories that barely provide groups with enough food to meet their caloric requirements during the dry season when fruit abundance is low. There may be a selective advantage to such infanticidal behavior if it helps prevent the formation of a new group on a resident group's territory, and the concomitant loss of space that would accompany such an event. *Received 15 November 2003, accepted 11 March 2003.*

Instances of infanticide have been reported for a number of different animal species (Stacey and Edwards 1983, Hausfater and Hrdy 1984, Hiraiwa-Hasegawa 1988). In many of these cases, infanticide was explained as a product of sexual selection in that it creates reproductive opportunities that otherwise would be lacking. One common scenario is that by killing unrelated young, the infanticidal male causes his breeding partner to produce new offspring that he fathers. Infanticide also has been reported in communally breeding groups in which males or females may destroy eggs or kill young of other group members, presumably to increase the odds that the infanticidal individual's offspring will thrive as a result of decreased competition with other young (Freed 1986, Whitmore 1986, O'Riain et al. 2000, Macedo et al. 2001).

Infanticide also has been reported among colonially nesting birds, where young are killed by neighbors (Fetterolf 1983, Hill et al. 1997). In colonially nesting species where cannibalism does not occur, it has been hypothesized that infanticide may be advantageous in that it prevents misdirected parental care or robbing of food by unrelated chicks (Pierotti and Murphy 1987, Pierotti 1991, Quinn et al. 1994), allows infanticidal individuals to obtain a nesting site that is in short supply (Morris and Chardine 1990, Hotta 1994), or may be a nonadaptive byproduct of aggressive territorial behavior (Hunt and Hunt 1975, Hunt and McLoon 1975).

Although mammals such as chimpanzees (*Pan troglodytes*) have been reported to kill young in other groups in what may be an example of intergroup breeding suppression (Hiraiwa-Hasegawa and Hasegawa 1994), no descriptions of such behaviors have been published for avian species. In this note, I describe an incident in which several members of a group of White-winged Trumpeters (*Psophia leucoptera*) killed the offspring of an intruding group that was breeding on their territory, and discuss whether this behavior might have any adaptive significance.

METHODS

Between 1983 and 1987, I conducted a study on the behavior and ecology of White-winged Trumpeters (Gruiformes, Psophiidae)

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living in the vicinity of Cocha Cashu Biological Station, in Manu National Park, Peru (11° 51′ S, 71° 19′ W). The study area was located in undisturbed lowland tropical moist forest (for a detailed description of study site, see Terborgh 1983). During the study I conducted 2,460 h of focal observations on individuals in 7 permanent territorial groups and 10 temporary nonterritorial groups that formed during four breeding seasons. The majority of birds observed were color banded and habituated to humans, allowing me to observe them at distances of ≤4 m for entire days. Because trumpeter groups were cohesive and interactions between groups were easily observed, any infanticidal event that occurred during focal observations should have been observed. However, because such events probably occurred infrequently and transpired rapidly, odds were low that an observer would have been present when such an attack took place.

RESULTS AND DISCUSSION

White-winged Trumpeters are cavity nesters. Their chicks are precocial and leave the nesting cavity the day after hatching to travel and forage with their groups on the forest floor. At Cocha Cashu, the majority of trumpeters lived in permanent territorial groups that defended contiguous territories with a mean size of 72 ha (Sherman 1995a). Permanent groups had a cooperatively polyandrous mating system in which multiple adult males mated with a dominant female who laid the only clutch (Eason and Sherman 1995). The mean size of permanent groups was seven, with groups typically consisting of a dominant male and female, beta and gamma adult males, a beta adult female, and the group's offspring that were two years of age or younger. All members of the group helped to feed and protect the group's chicks and guarded them closely until they began to fly at about six weeks of age. Occasionally, temporary nonterritorial groups would form during the breeding season and attempt to nest on a permanent group's territory. These groups had a mean size of three individuals and usually disbanded several months after forming (Sherman 1995a).

During the 1984–1985 breeding season, a temporary group composed of two females and a male formed on a permanent group's territory and successfully fledged two chicks. Unlike all other temporary groups observed, this group (hereafter referred to as the intruding group) did not disband. During the 1985–1986 breeding season, the intruding group, which now consisted of the original trio, their two offspring, and a new adult male, incubated their clutch in a nesting cavity inside the edge of the permanent group's territory. Four days after the intruding group's chick hatched, the two groups began to interact daily near this nesting cavity. These interactions consisted of the permanent group hearing the intruding group at a distance and responding with 5–10 min of territorial calling, to which the intruding group responded in kind. The groups remained separated by a distance of 70–100 m during these interactions. When trumpeter groups lacked young chicks, permanent groups directly confronted intruders, running toward them and chasing them to the closest territorial boundary (Sherman and Eason 1998). Long distance interactions between groups occurred most often when trumpeter groups had chicks that were unable to fly.

After three days of long distance interaction, five of the seven adults in the permanent group approached the intruding group on the morning of the fourth day. These individuals chased the intruding group, and then the two groups exchanged territorial calls while separated by about 10 m. The intruding group's 7-day-old chick was 90 m from the interaction and was guarded by the group's dominant male and beta female. This chick weighed about 140 g (11% of mean adult weight) and although unable to fly, could run rapidly. I was unable to locate the permanent group's 21-day-old chick and the dominant female and delta male that presumably were guarding it for the duration of the territorial interaction.

After 18 min of interaction, the intruding group's chick started giving repeated severe distress calls, shortly after which two adults gave high intensity alarm calls. The members of the two groups that had been calling ran 90 m to the chick, where three permanent group birds (the dominant male, gamma male, and a subordinate female) were forcefully and repeatedly pecking its chest while it lay on its side on the ground. After giving distress calls for 45 s the intruding group's chick fell silent

and remained motionless. The three permanent group birds continued to repeatedly peck the chick's chest with great force for an additional 75 s. At this time the chick was still breathing but appeared unconscious. For the next 12 min, the permanent group's dominant, beta, and gamma males took turns standing over the chick while the two groups continued to exchange territorial calls. The intruding group then stopped calling and left. When it returned 30 min later, its chick was dead and the members of the permanent group, which were preening 30 m away, chased the group away one last time.

I collected the intruding group's chick at the end of the day and found that its only apparent injury was a puncture wound just below the sternum that was 0.35 cm in diameter. The liver was punctured and a blood clot approximately 1.0 cm in diameter had formed on it. There did not appear to be enough blood on the chick or the ground to indicate that it had bled to death, suggesting that perhaps it died of shock.

The adults' behavior during their attack on the chick was unprecedented. During territorial interactions, trumpeters occasionally engaged in bouts of sparring, during which pairs pecked and kicked at each other but rarely made contact. On those rare occasions when one bird knocked another to the ground, the downed individual would be chased off, not repeatedly attacked. The ganging up of a group of birds on a single individual and the sustained level of aggression during which the chick was repeatedly pecked for 2 min were behaviors that were not seen at any other time during this study.

The hesitancy of groups with young flightless chicks to engage in direct confrontations with other groups suggests that trumpeters may perceive some risk associated with such interactions. The loud territorial calls given during such interactions can be heard by humans more than 300 m away, and are likely to make groups more conspicuous to predators. However, when groups with young chicks interact with other groups, it is not territorial calls that are avoided, but contact with the opposing group.

The proximate cause of the attack could have been the presence of an unfamiliar chick, the incapacitation of an intruding individual, or some other cue. The adults' aggressive response might be adaptive if it prevented the adoption of an unrelated chick and the resultant cost of misplaced parental care. Instances of infanticide that may be linked to preventing misplaced parental care have been reported for various species in which there are numerous opportunities for dependent young to enter new groups (Pierotti 1991). However, because trumpeter groups occupy such large territories, breed asynchronously during the six-month rainy season, and rarely come into contact with other groups when they have young chicks, the opportunity for chicks to switch between groups is rare. Furthermore, the rapid growth of young chicks and their steady change in plumage make it possible to discriminate individuals that differ in age by only a few days (Sherman 1995b).

The potential benefit of such an attack might be greatest for a permanent trumpeter group that is attempting to prevent a temporary group from becoming established on part of its territory. White-winged Trumpeters are highly frugivorous, with the pulp of fallen fruit providing about 90% of mean daily energy intake. Fruit removal experiments suggest that territory size reflects the area needed for group members to meet their minimum daily caloric requirements during the dry season when fruit abundance is low (Sherman and Eason 1998). A substantial reduction in territory size would lead to the emigration of subordinate adults, who are excluded from limited food resources by dominant individuals, from a permanent group. This would likely result in the continued shrinking and eventual loss of the group's territory as smaller groups are dominated by larger groups during territorial interactions (Sherman 1995a).

The failure of a temporary group to breed successfully may help lead to its disbanding. Four months prior to the attack, a different trio of birds incubated their clutch on the opposite end of the permanent group's territory. The permanent group fought with this trio almost daily, flying up to evict the incubating bird from the nesting cavity and then chasing the group away from the nesting site. The chick that fledged from this group's clutch disappeared for unknown reasons when it was about two weeks old and the group disbanded six weeks later.

Of the 10 temporary groups that formed during four breeding seasons, nine disbanded within 4 months and lacked chicks when they disbanded. Unlike the adults in these groups, no chicks <1 year of age were ever observed to immigrate into new groups or fend for themselves outside a group, and thus available evidence suggests that all nine groups failed to reproduce successfully. A group such as the intruding group that increased its size through successful reproduction and retention of young would have an increased likelihood of being able to establish and defend a new territory. By the end of this study the intruding group had the same mean group size as permanent groups at the study site and had succeeded in taking over about 25% of the permanent group's territory as well as portions of two other groups' territories. An equivalent loss of territory to a second intruding group would likely lead to the collapse of the permanent group unless they were able to acquire additional space from neighboring groups. The infanticidal behavior described here could confer a selective advantage if it helped prevent the breeding and establishment of a temporary group on a permanent group's territory.

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Evaluation of the Moisture-Facilitated Nest Depredation Hypothesis in a Semiarid Environment

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ABSTRACT.—We evaluated the moisture-facilitated nest depredation hypothesis in a semiarid environment in the Southern High Plains of Texas during 1999 and 2000. Scaled Quail (*Callipepla squamata*) provided an excellent model species for this evaluation because they typically suffer significant nest mortality and inhabit semiarid to xeric environments. We monitored 102 nests until they either hatched or were predated. Nest mortalities occurred on 30 days and precipitation fell on 51 days during the two-year study. Stepwise logistic regression revealed a predictive relationship for a model with central precipitation on the day of nest predation as a predictor. However, in contrast to our predictions, the equation indicates precipitation is negatively associated with nest predation in this data set. Thus, our data do not support the moisture-facilitated nest depredation hypothesis for Scaled Quail in the semiarid, Southern High Plains of Texas. *Received 29 October 2002, accepted 10 March 2003.*

Precipitation has been linked widely to population size in birds (Roseberry and Klimstra 1984, Heffelinger et al. 1999, Shou-Hsien and Brown 1999). Precipitation in appropriate amounts and intervals is necessary for surface water and vegetative growth to supply food and cover (Guthery et al. 1988, Briggs and Knapp 1995, Fahnestock and Detling 1999). Also, excessive precipitation at inappropriate times can cause flooding and result in nest mortality (Espie et al. 1998). Predation, however, is the primary cause of nest mortality (Ricklefs 1969, Martin 1993). Several investigators (Palmer et al. 1993, Roberts et al. 1995) have suggested a link between nest predation and precipitation. They hypothesized (the moisture-facilitated nest depredation hypothesis) that moisture may increase scent production of incubating hens, thereby increasing the searching efficiency of many mammalian nest predators. Microbial growth is believed to be the primary cause of scent production (Syrotuck 1972). An increase in moisture on the incubating bird or the nest during periods when temperatures are sufficient for microbial growth, should cause increased scent production and facilitate location of nests by predators.

The moisture-facilitated nest depredation hypothesis is supported by several studies that report a positive relationship between rainfall and nest predation on Wild Turkeys (*Meleagris gallopavo*; Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998). These studies occurred in relatively mesic areas where climatic conditions might be expected to keep substrates for microbial growth relatively moist despite lack of rainfall events (Bailey 1998). In more semiarid environments, precipitation events should provide more discrete periods of increased microbial growth and thus scent production, because substrates for microbial growth will desiccate more rapidly in semiarid environments than in mesic environments. Thus, the relationship between moisture and predator efficiency may be amplified in semiarid environments. Our objective was to evaluate the moisture-facilitated nest depredation hypothesis in a semiarid environment. Scaled Quail (*Callipepla squamata*) provided an excellent model species for this experiment.

METHODS

We conducted this study on approximately 12,000 ha in southern Cochran County, Texas (centered on 33° 43′ N, 102° 46′ W). Most of the study area consisted of rangeland with scattered scrub mesquite (*Prosopis glandulosa*), cholla cactus (*Opuntia* sp.), and yucca

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(*Yucca* sp.), or shinoak (*Quercus havardii*) on the more sandy sites, with portions adjoining farmlands and fields in the Conservation Reserve Program. The climate was semiarid, warm, and continental, characteristic of the Southern High Plains of Texas (Newman 1964). The long term mean annual precipitation is approximately 42 cm, with high wind velocities, high summer temperatures, and low humidity, and is characterized by rapid changes and extremes in temperature and amount of rainfall (Newman 1964). More than 80% of the annual precipitation occurs during the warmer half of the year (May through October).

Potential mammalian nest predators in the study area included badgers (*Taxidea taxus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), feral cats (*Felis cattus*), hispid cotton rats (*Sigmodon hispidus*), southern plains wood rats (*Neotoma micropus*), spotted ground squirrels (*Spermophilus spilosoma*), striped skunks (*Mephitis mephitis*), and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). Potential reptile predators included coachwhip snakes (*Masticophis flagellum*), bullsnakes (*Pituophis melanoleucus*), and western hognose snakes (*Heterodon nasicus*; Schemnitz 1994).

We trapped Scaled Quail hens from February through mid-April during 1999 and 2000 using walk-in funnel traps (Smith et al. 1981) baited with millet and cracked corn, and fitted each bird with a 6.5-g necklace style transmitter (American Wildlife Enterprises, Monticello, Florida) without a body loop. We located radio-marked hens ≥4 times per week and determined the fate of their nests from mid-April through August during 1999 and 2000. We categorized nest fate as predated or successful. A nest was deemed successful if any of the eggs hatched.

The moisture-facilitated nest predation hypothesis predicts that nest predation events should be associated with periods when precipitation increases microbial growth and thus scent production. Nests could be predated during the egg laying, incubating, or hatching stages. Scent production of hatching nests should be greater than those of nests in the egg laying or incubating stages because of the exposed egg membranes and drying chicks. This increase in scent production along with chick vocalization (Briskie et al. 1999) and increased activity of hen and chicks (Martin et al. 2000) that results as the clutch hatches, provides predators with more cues to locate the nest and thus a greater risk of predation than incubating nests. Consequently, successful hatching events should be associated with relatively drier periods because successful nests are not detected despite the increased cues the hatching process provides to predators.

Moistening effects of precipitation in our study area during the dates of incubation are relatively short. Relative humidity can decrease 50% or more within a few hours following thunderstorm dissipation in the Southern High Plains of Texas (Bomar 1995). Fine materials such as feathers or dried grasses in nests lose moisture to the air and reach equilibrium within 1–2 h (Countryman 1971). Thus, desiccation of moisture holding substrates would occur generally within 24 h after cessation of precipitation. Significant microbial growth could occur, however, within this time frame (Dabbert et al. 1996). We used stepwise logistic regression to examine the relationships between nest fate and the amount of precipitation falling on the day before nest conclusion and the amount of precipitation falling on the day of nest conclusion. We obtained precipitation data (National Oceanic and Atmospheric Administration 2003) from a central weather station at Morton, Texas (33° 43′ N, 102° 46′ W) that was located <20 km from all nests. It is possible, however, that weather events recorded at the central station might not impact all nests because precipitation events in this region can be localized. Precipitation events typically develop west of the study area and move eastward for many kilometers (Bomar 1995). Gaps in precipitation coverage on the study area are generally north or south of the front. We used precipitation data from two secondary weather stations that exceed the northern (Muleshoe, Texas; 33° 57′ N, 102° 47′ W) and southern (Plains, Texas; 33° 11′ N, 102° 50′ W) boundaries of the study area to create a variable representing widespread precipitation to address this problem. We calculated widespread precipitation as the mean amount of precipitation detected at the three (central, northern, and

TABLE 1. Precipitation associated with nest predation and hatching events for Scaled Quails during 1999 and 2000 in the Southern High Plains of Texas. Precipitation was negatively associated with nest predation, and thus does not support the moisture-facilitated nest depredation hypothesis.

	Predation (n = 43)		Hatching (n = 59)		Mann-Whitney	
Variable	Mean	SE	Mean	SE	U	P
Central[a]						
Day before event	0.25	0.11	0.26	0.11	1,264	0.967
Day of event	0.10	0.05	0.40	0.14	987	0.009
Widespread[b]						
Day before event	0.44	0.14	0.36	0.11	1,233	0.765
Day of event	0.04	0.03	0.13	0.04	1,008	0.007

[a] Data from one central weather station within the study area.
[b] Data from three weather stations: one within the study area and one each beyond the northern and southern boundaries of the study area; mean values were used to characterize regional precipitation.

southern) weather stations during the same 24-h period. The amount of widespread precipitation for the day before nest conclusion and for the day of nest conclusion were included in the stepwise logistic regression analysis with the variables from the central weather station. We constructed the data set so that the analysis would solve for the predated nest outcome and set the criterion for inclusion of a variable at $P \leq 0.20$ to prevent exclusion of potentially important predictor variables (Hosmer and Lemeshow 2000). We interpreted logistic regression coefficients by stating odds ratios. We used Mann-Whitney U-tests (SPSS, Inc. 2002) to illustrate differences in central and widespread precipitation variables between predated and successful nests.

RESULTS

We monitored 83 females and their 102 nests from 18 May to 29 August 1999, and 19 May to 27 August 2000. Nest mortalities occurred on 30 days and precipitation fell on 51 days during these two sampling periods. Stepwise logistic regression revealed a predictive relationship ($\chi^2 = 4.037$, df = 1, $P = 0.45$) for a model with central precipitation on the day of nest predation as a predictor ($\beta = -0.660$, SE = 0.413, $W = 2.559$, df = 1, $P = 0.11$, odds ratio = 0.517). However, in contrast to predictions of the moisture-facilitated nest predation hypothesis, the equation indicates precipitation was negatively associated with nest predation in this data set. Nests were 48% less likely to be predated with each 1-cm increase in precipitation. Central precipitation on the day before nest predation ($P = 0.98$), and widespread precipitation on the day before ($P = 0.74$) and the day of ($P = 0.81$) nest predation were not significant predictors of nest predation. The relationship identified in the logistic regression analysis is further illustrated by greater mean precipitation values for hatching events compared to predation events (Table 1). Thus, our data do not support the moisture-facilitated depredation hypothesis for Scaled Quail in the semiarid, Southern High Plains of Texas.

DISCUSSION

It is unclear why our results differ from those obtained from Wild Turkeys in Mississippi (Palmer et al. 1993) and New York (Roberts et al. 1995, Roberts and Porter 1998). One reason may be that the community of predators is different among study areas. Most predators in the Mississippi and New York studies were medium-sized mammals (Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998). While we were not able to identify all nest predators in our study area, some were snakes. Snakes use a vomeronasal system to sense prey (Halpern 1992) and can detect and respond to odors related to bacterial growth (Jojola-Elverum et al. 2001). It is unclear, however, how this system is affected by increases in environmental moisture. Also, differences in body size and thus scent production between Scaled Quail and Wild Turkeys, and differences in nest site construction and placement, could change the cues predators use to aid in their search for nests. Sus-

tained periods of low humidity in our study area create a different environment in which predators search for nests, compared to the prolonged periods of relatively high humidity common in eastern North America (Bailey 1998). Future studies should examine these issues.

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Novel Nesting Behavior in Cave Swallows

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ABSTRACT.—The Cave Swallow (*Petrochelidon fulva*), first discovered breeding in Texas in 1915, originally was thought to be confined to sinkholes in central and western Texas. During our survey of bridges in Brazos County, Texas, we discovered Cave Swallows modify and use old Barn Swallow (*Hirundo rustica*) nests, a previously unreported behavior. The presence of Barn Swallows (or old Barn Swallow nests) may facilitate colonization of new areas by Cave Swallows. *Received 24 January 2003, accepted 20 November 2003.*

Discovered in 1915, the Cave Swallow (*Petrochelidon fulva*) population in Texas occurred historically only in sinkholes in the Edwards plateau region and caves in western Texas (Selander and Baker 1957). This population recently expanded its range to include most of southern and central Texas (Martin 1974, Martin and Martin 1978). Martin and Martin (1978) suggested that a shift toward the use of nest sites other than caves facilitates range expansion, and by using these structures the species may become common in areas where it had been absent. However, previous studies did not address the presence of other swallow species as a possible precursor for colonization.

During 2001 we studied Barn Swallows (*Hirundo rustica*) and Cave Swallows nesting in Brazos County, Texas (30° 40′ N, 96° 18′ W). We searched 21 bridges and 18 culverts from 8 to 29 April, which corresponds to the peak breeding season in our study area, and collected nest morphology data from nests on eight highway bridges. Cave Swallows build mud nests that do not incorporate vegetation (unlike Barn Swallows), and we expected to locate two types. The most common type consists of an open, flattened cup with a wide rim; in the less common type the sides of the nest flare up and almost enclose the cup, leaving a chimney-like opening (West 1995). These nests are built entirely by Cave Swallows and here we refer to them as "original." We discovered a third type and refer to this as a "modified" nest. A modified nest is an old Barn Swallow nest modified and used by Cave Swallows. In recently modified nests, Cave Swallows lay eggs in the Barn Swallow nest cup (which can include vegetation, horse hair, and feathers) and only add mud to produce the wide rim. Over time, mud accumulation occurs and the Barn Swallow nest serves as the foundation; in older modified nests the eggs are laid on the mud bottom of the nest.

We found 52 active Cave Swallow nests, and all were under bridges that also contained active Barn Swallow nests. Sixteen (31%) were original nests, while 36 (69%) were modified nests. Modified nests represented between 20% and 97% of active Cave Swallow nests within a colony. Mean height of modified nests (including the Barn Swallow portion) was 21.3 cm and ranged from 8.0 to 50.8 cm.

We found no records of nest modification by Cave Swallows in a review of the limited papers available on the species' reproductive biology. Swallow species, especially those that build mud nests, are closely related and have similar nesting behaviors (Winkler and Sheldon 1993). All species reuse nests, which tend to be well protected and can remain intact for several years, and they commonly repair old nests before laying eggs (Barclay 1988, West 1995, Brown and Brown 1996). Although nest substrate and placement is similar among species, Samuel (1971) noted that 12% (9/73) of Cliff Swallow (*Petrochelidon pyrrhonota*) nests were built on top of Barn Swallow nests in West Virginia.

We believe that the presence of artificial structures alone does not adequately explain

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the observed range expansion of Cave Swallows in Texas. We suggest that the presence of Barn Swallows and their nests may be a necessary precursor for Cave Swallow colonization of new breeding areas. Settling in established Barn Swallow colonies assures the presence of essential resources (e.g., food, nesting materials) while nest modification affords a foundation upon which to place a nest, thus saving both time and energy.

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Body Sway Foraging by a Yellow-crowned Night-Heron

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ABSTRACT.—We observed a Yellow-crowned Night-Heron (*Nyctanassa violacea*) with its belly partly submerged in water, rapidly swaying its body laterally while holding its head and most of the extended neck still above the water. This behavior was observed several times with "Stand and Wait, Walk Slowly, Stand and Wait" foraging among three episodes of the "Submerge and Sway" mode. This body swaying motion appeared to flush out a frog that the heron captured during the second episode. *Received 7 January 2003, accepted 23 April 2003.*

On 6 March 2002, at Corkscrew Swamp Sanctuary, Collier County, Florida (81° 41′ W, 26° 22′ N), we observed an adult Yellow-crowned Night-Heron (*Nyctanassa violacea*) for about 5 min beginning at 09:20 EST at distances of 1–4 m from the boardwalk that traverses the sanctuary. After engaging in a series of "Stand and Wait, Walk Slowly, Stand and Wait" foraging behaviors (Rodgers 1983) in water estimated to be 7–10 cm deep, the bird immersed its belly in the water and extended its head and neck forward, level with and above the water surface. This neck extension was followed immediately by a rapid lateral body swaying of about 15 cm for a period of about 0.8 s. This behavior was repeated for about 6–8 s, producing concentric circles of waves on the water surface emanating from the body. During this swaying behavior we did not detect movement of the head and upper neck. After this first episode of "Submerge and Sway" behavior the heron stood, walked slowly about 1 m, then paused and did a second "Submerge and Sway" sequence, during which it caught and ate a small frog

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that apparently was flushed from beneath or near the bird's body. The frog was caught directly in front of the bird. The heron then performed several "Stand, Walk Slowly, Stand" behaviors alternating with the "Submerge and Sway" movements before disappearing from view.

Head and neck swaying behavior occurs in ardeids and has been suggested to aid depth perception (Kushlan 1978, Sibley et al. 2001). Because the heron we observed held its head and most of its neck stationary, the depth perception function cannot explain its behavior. We suggest the body sway behavior was used to flush prey, enabling the bird to detect prey attempting to escape the disturbance created in the shallow water. The bird most likely would detect escaping prey within 180° forward of the body. Such flushing may be particularly efficient in shallow water. Ardeids rarely wade in deep water and have not been reported to dive (Watts 1995) or bathe (Mock 1976). Parmer (1968) reported an immature Yellow-crowned Night-Heron hovering over water and catching a fish. Kushlan (1978) described 38 feeding behaviors in wading birds with 5 of those recorded for Yellow-crowned Night-Herons: Standing, Head-swaying, Neck-swaying, Pecking, and Walking Slowly. Watts (1995) added Running but regarded the Yellow-crowned Night-Heron as the least active among eight species of North American herons. Martinez-Vilalta and Motis (1992) named "Swimming Feeding" as a foraging behavior of the Black-crowned Night-Heron (*Nycticorax nicticorax*), but did not describe or explain it.

The behavior we observed may be an example of "insight learning" (Welty and Baptista 1988). Innovative, complex feeding behavior has been documented in several avian species, including a Green Heron (*Butorides virescens*) luring fish with bread (Lovell 1958) and other baiting behaviors (Davis and Kushlan 1994, Sibley et al. 2001), New Caledonian Crows (*Corvus moneduloides*) manufacturing hooks to retrieve food (Hunt 1996, Hunt and Gray 2002, Weir et al. 2002), and Lesser Antillean Bullfinches (*Loxigilla noctis*) recognizing and opening sugar packets (Reader et al. 2002). Welty and Baptista (1988) summarized other examples of innovative, insight behaviors.

S. C. Stein (pers. comm.), a member of the Corkscrew Sanctuary staff, questioned other staff and volunteers on our behalf and found no one who had observed this behavior. However, on 11 December 2002, JL visited Corkscrew Swamp Sanctuary and was told by two volunteers that "Body Sway Foraging" recently had been observed on several occasions. Now that attention has been called to this behavior, it will be interesting to see if and when it is observed elsewhere.

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Ornithological Literature

Edited by Mary Gustafson

BIRDS OF NEBRASKA: THEIR DISTRIBUTION AND TEMPORAL OCCURRENCE. By Roger S. Sharpe, W. Ross Silcock, and Joel G. Jorgensen. The Univ. of Nebraska Press, Lincoln. 2001: 520 pp., 21 color plates, 4 maps. $69.95 (cloth).—For many ornithologists and birders, mention of Nebraska conjures up images of vast flocks of Sandhill Cranes (*Grus canadensis*) settling in to roost on the Platte River, or of the hordes of waterfowl and shorebirds stopping on the shallow wetlands in the Rainwater Basin during spring migration. However, a closer look reveals that Nebraska has a surprisingly rich avian diversity (437 species, including 236 that breed), greater than most of the surrounding states.

Birds of Nebraska contains a wealth of information about Nebraska's birds and varied habitats, and is certainly the definitive reference on the avifauna of this state. The layout of the book is logical and flows smoothly. It begins with an interesting overview of Nebraska's geological history and climate, followed by a thorough discussion of the state's major habitats, both historical and present day, including an excellent color photo of each. Next is a thorough section on the history of ornithology in Nebraska, dating back to the Lewis and Clark expedition's visit in 1804. I found this section fascinating, both in terms of the richness of early ornithological work in Nebraska and from the sheer volume of work done in the state during the last two centuries. The species accounts comprise the bulk of the text and include standard information for each species: (1) status; (2) documentation, which in most cases references the voucher specimen, often for multiple subspecies; (3) taxonomy, including any known subspecies that have occurred in the state; (4) distribution and ecology, providing basic habitat information, arrival and departure dates, nesting information, peak counts, and much more; and (5) general tips on finding each species in Nebraska.

If there is one feature of this book that makes it stand out among other state and provincial bird references, then it must be the level of taxonomic detail that is included. Where appropriate, the species accounts include all known information about the seasonal occurrence and distribution of known subspecies and identifiable forms. The White-breasted Nuthatch (*Sitta carolinensis*) account is a fine example. The eastern subspecies *S. c. cookei* is widespread in the eastern two thirds of Nebraska, and reaches farther west along the North Platte River. The Rocky Mountain subspecies *S. c. nelsoni* breeds in the Pine Ridge in northwestern Nebraska. Both subspecies are essentially resident and are best identified by vocalizations. A few *S. c. cookei* regularly wander west to the Wyoming border. Wandering away from breeding areas by *S. c. nelsoni* is poorly documented in Nebraska. With this information in hand, birders and ornithologists can focus on better understanding distributional patterns of these subspecies, which may someday be elevated to full species status. The species accounts are peppered with this level of detail, and this is surely one of the strengths of this book.

In addition to the level of taxonomic detail, this book has other strengths. It includes records from just a few months prior to publication, meaning that the book is up to date. For many species, their patterns of occurrence differ between eastern and western Nebraska, largely the result of elevation and subspecific variation. Where appropriate, the authors have included basic information (e.g., arrival and departure dates) that reflects these longitudinal differences.

A shortcoming of this book was the decision not to include range maps. The species accounts include very detailed descriptions of distribution, particularly for breeding species, but even the best description cannot compete with a good map. Further, what makes this an even bigger disappointment is the realization that the ranges of so many east-west species pairs, e.g., Indigo (*Passerina cyanea*) and Lazuli (*P. amoena*) buntings, meet or overlap in Nebraska, and that a map illustrating these

distributions would be extremely informative. Maps may not be necessary for migrants or vagrants, but are missed for breeding species.

Other than the lack of the maps, this book has few shortcomings. A few of the arrival and departure dates seemed questionable, and I wondered if tougher standards should have been applied when reviewing some of these dates. For example, the spring arrival dates given for the Common Nighthawk (*Chordeiles minor*) are all in the first 10 days of April, in stark contrast to arrival dates that are 1–2 weeks later in surrounding states to the east and south. Information in the Finding section of some species was scant, but I realize that this was not intended to be a bird finding guide.

From professional ornithologist to casual field birder, this reference offers a wealth of useful information about Nebraska's birdlife. The meticulous species accounts, up to date information, detailed summary of Nebraska's ornithological history, and basic birding tips will make this book an invaluable addition to any library.—STEPHEN J. DINSMORE.

DUCK BANDING. By Norman North. Canadian Wildlife Service, Bird Banding Office, Carleton Univ., 1125 Colonel By Dr. (Raven Rd.), Ottawa, ON K1A 0H3, Canada. 1997 (English version), 2001 (French version): 29-minute video. Available at no cost from CWS Bird Banding Office.—This is an excellent introduction to late summer (and other) duck banding. It includes a general overview of sex and age characteristics with illustrations of 19 species of ducks and one hybrid, shows and discusses a variety of trap designs plus trapping techniques and site selection, and covers banding equipment and procedures as well, all in 29 minutes. As indicated at the beginning of the film, there are many exceptions to the general information provided, particularly in regard to the sex and age identification of some species. As I watched the species section I kept thinking of the exceptions that I have seen to the characteristics mentioned and the plumages shown as typical. The caution about the need to work with an experienced, knowledgeable bander when starting out cannot be overemphasized, and it is included here appropriately. This is primarily a video to be shown to a group for prebanding orientation and, especially with commentary by the group leader(s) who can expand on certain points, it accomplishes this admirably.—ELWOOD (WOODY) MARTIN.

ALL WEATHER HAWK WATCHER'S FIELD JOURNAL. By Donald S. Heintzelman. J. L. Darling Corp., Tacoma, Washington. 2002: 64 pp. $7.95 (spiral bound, plastic cover).—I was introduced to Rite-in-the-Rain all-weather field notebooks while collecting data on shrikes in Florida. There were too many days when I came home with my data sheets soggy from sudden thunderstorms that caught me in the field. The frustration of transferring data onto dry sheets or literally having the day's work washed out, is great. This all changed the day I was given an all-weather notebook. I no longer carry sheets of paper or clipboards in the field, and these notebooks also are ideal for travelogues.

Donald Heintzelman had the right idea when he teamed up with the Rite-in-the-Rain team to put out the *Hawk watcher's field journal.* Many hawk watchers have had similar frustrations with soggy notes, especially in the tropics. This raptor journal version of the all-weather notebook will allow raptorphiles to record their observations and data, knowing they will be safe for years to come. The 18 × 12 cm diary is comfortable to hold and small enough to fit in a pocket.

The first page has room for personal information and the dates of use. There also is a reminder that raptors are protected and a statement on their conservation. Next follows a checklist of the birds of prey of North and Central America and West Indies. The remaining 59 pages are designed for recording data. At the top of each page are spaces for recording location, date, visibility, temperature, wind speed and direction, distance traveled (for those conducting transects), cloud cover, starting and ending times, and GPS location. This format helps the observer remember to record these data, which often are overlooked and then lacking at the end of a study.

Using the notebook here in the desert at Eilat, I found the light blue lines (and my writing) difficult to see in the glare. Also, the fact that each page is limited to the number of preprinted lines makes it impractical for making hourly hawk migration counts. However, I highly recommend this notebook for those who keep detailed field observations or a diary of field trips; those notes can be stored safely as archival data.—REUVEN YOSEF.

Memorial

Wilson Bull., 115(3), 2003, pp. 354–356

Richard H. Pough (1904–2003)

Richard Pough at the Jersey shore, May 1940. Photograph by C. W. Mauzer.

Richard Hooper Pough, the foremost land preservationist of his time and a versatile innovator in bird conservation, died at his home in Chilmark, Martha's Vineyard, Massachusetts, on 24 June 2003. During his 99 years he left his mark on such institutions as the National Audubon Society, the American Museum of Natural History, and The Nature Conservancy (of which he was a founder and the first president). The series of bird guides he produced in the 1940s and 1950s was ahead of its time, complementing Roger Tory Peterson's groundbreaking guides with the inclusion of material on food, breeding, and conservation.

Pough (pronounced POE) was not an "in your face" preservationist. Rather, he was a wheeler-dealer land developer turned inside out, a gentle Alexander who preempted for protection of large areas of eminently exploitable land with original thinking and other people's money. "I don't protest anything," he said. "If someone comes to me and complains that a majestic forest is about to be cut, I ask, 'Are you a man or a mouse? Go out and buy it!'" Sanctuaries such as Pennsylvania's Hawk Mountain, Florida's Corkscrew Swamp, Arizona's Arivaipa Canyon, and South Carolina's Congaree Swamp are among the multitude of open spaces and wildlife habitats he persuaded the affluent to buy and preserve.

Pough was born in Brooklyn, New York, on 19 April 1904, of parents who stimulated his curiosity about almost everything. His father, Francis Harvey Pough, was a chemist with a deep interest in geology and mineralogy. His mother, Alice Becker Pough, studied biology and public health at the Massachusetts Institute of Technology. Summers on Block Island, off Rhode Island, ignited the boy's lifelong interest in birds. He was a graduate of MIT (followed by a year of fine arts at Harvard) and in his early adult years worked as both a chemist and a mechanical engineer.

However, in 1932 a move to Philadelphia, where he operated a chain of photographic supply stores, changed his life. His early interest in birds had persisted. He became curious about why George Miksch Sutton, in an article in *The Wilson Bulletin,* had available

the data on a very large number of bands taken from dead Northern Goshawks (*Accipter gentilis*) found near Drehersville, Pennsylvania. A visit to the area appalled him. Hunters assembled on Hawk Mountain in autumn to shoot (and leave to rot) thousands of migrating raptors. He campaigned against the slaughter and, in a well-to-do New Yorker named Rosalie Edge, found an individual to buy and put off limits to hunters what has become a celebrated famous hawk-watching station.

His achievement at Hawk Mountain brought him employment by the National Audubon Society in 1936 to keep an eye on "persecuted species." His wife Moira often provided the clue that sent him into action. When Pough identified the feather ornamenting her new hat as that of a Golden Eagle (*Aquila chrysaetos*), he turned feather detective in a big way and helped snuff out during the 1940s a resurgence of the trade in wild bird plumes.

At about the same time, Moira spotted an advertisement for the sale of "California linnets" by a large department store. Pough recognized the "linnets" as House Finches (*Carpodacus mexicanus*), then unknown as wild birds in the eastern U.S., and discovered a flourishing trade in them around New York City. Federal agents alerted by Pough issued summonses, prompting nervous pet dealers to give the birds their freedom. So began the "invasion" of the House Finch outside its western range.

Pough's fertile mind created the stuff of ornithological legend. When a Canadian retiree in Florida named Charles Broley expressed his restlessness to him, Pough suggested that he start a banding program to shed light on the Bald Eagle's (*Haliaeetus leucocephalus*) movements in and out of the state. The 58-year-old Broley became an expert tree climber, clambering as high as 35 m and banding more than 1,200 eagles before he died. (Pough said that Broley fell only once, off a chair when trying to reach his climbing equipment in a closet.)

In fact, Pough seemed to be almost everywhere. He spent two months in Louisiana's Singer Tract, monitoring a female Ivory-billed Woodpecker (*Campephilus principalis*) that was unable to find a mate. He was among the first to warn publicly of DDT's menace to wildlife. After leaving Audubon, he designed a baffle that kept aggressive White-tailed Tropicbirds (*Phaethon lepturus*) from the burrows of the smaller and critically endangered Bermuda Petrels (or Cahows; *Pterodroma cahow*).

Meanwhile, Pough was writing his series of field guides. The first, *Audubon bird guide,* covered the small land birds of eastern and central North America and was published in 1946. *Audubon water bird guide* appeared in 1951, and *Audubon western bird guide* in 1957. Prompted by his meager Audubon salary and an occasional confrontation with the society's strong-willed president, John Baker, he defected to the American Museum of Natural History in 1948, becoming chairman of its Dept. of Conservation and General Ecology. A friend, aware that he had not received an advanced degree, asked Moira why so many people at the museum greeted him as "Dr. Pough." "Dick's doctorate was conferred on him by the elevator operators," Moira explained. "They just assumed that a person with a position like his must be a Ph.D."

The pseudo-Dr. Pough made his move into land acquisition. When he learned that the federal government planned to sell Great Gull Island off New London, Connecticut, he recalled that it had been the site of an important tern colony before the U.S. Army built a fort there. He persuaded the museum to buy the island, which became, under its director Helen Hays, a center of tern research.

One of Pough's initiatives was to organize a series of "round table" luncheons under the museum's auspices, to which he invited Garden Club members from all over the metropolitan area. He gave them pep talks on the value of conserving open space in suburbia and beyond. "Garden Club leaders form the elite in a community," he explained. "They provide you with an entry to the sources of power."

His work led him in the 1950s to the Ecologists' Union, a group of professionals interested in preserving unique ecological areas, but whom Pough felt were simply bumbling along. He convinced them to change the organization's name to the Nature Conservancy. (Nonspecialists didn't know the meaning of

ecology, he argued.) At the same time he persuaded Lila A. Wallace, a founder of the Reader's Digest, to establish a $100,000 revolving fund to encourage local preservationists to act quickly when desirable land became available. Pough served as the new organization's founding president from 1954 to 1956. He then set out on his own. Creating an umbrella organization called the Natural Area Council, he lined up support from his old Garden Club contacts, who led him to a variety of men and women laden with an excess of both land and taxes. Beguiled by his charm, these landowners eventually turned over more than $15 million worth of property at 1960s prices. Before less affluent audiences, Pough went into his "man or mouse" speech, dispensing advice on where to seek funding, what pitfalls to avoid, and how to upset a deal on which land developers seemed to have a lock.

His greatest strength lay in the friendship he struck up with Katharine Ordway, heiress to an immense fortune through the Minnesota Mining and Manufacturing Company (3M). She established the Goodhill Foundation, sent millions his way, and ensured the protection of land (notably under-appreciated prairie tracts) all over the country. Pough became the foundation's president after Ordway's death, and he and fellow trustees eventually distributed nearly $55 million as partial payment for areas of ecological value.

"What's in it for you?" was a question not applicable to Dick Pough. He prided himself on not making a penny from any of his countless transactions and said that as a freelance he paid himself an annual salary never exceeding $25,000. Yet he was no shrinking violet when it came to asking other people to give their money to save an exquisite expanse of land. He also knew that to promote his causes, he had to promote himself. Some years ago, at the urging of a friend, he called a magazine editor to lobby for the inclusion of that friend as a subject in a series of articles the magazine was publishing on prominent conservationists. The editor explained that the person in question was not a suitable subject for the series. "Then how about me?" Pough instantly shot back.

His wife, Moira, died in 1986 and their son, Edward, in 2000. He leaves two brothers, Frederick and Harold, a son Tristram, two daughters-in-law, Victoria and Marguerite, two grandchildren and, not so incidentally, swatches of unspoiled America whose acreage not even Dick Pough himself was able to calculate.— FRANK GRAHAM, JR.

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Barry Kent MacKay

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PIRACY AS AN IMPORTANT FORAGING METHOD OF APLOMADO FALCONS IN SOUTHERN TEXAS AND NORTHERN MEXICO

JESSI L. BROWN,[1,2] ANGEL B. MONTOYA,[1] ERIN J. GOTT,[1] AND MARTA CURTI[1]

ABSTRACT.—Piracy (kleptoparasitism) accounted for 14% of observed foraging attempts on vertebrates (n = 125) by Aplomado Falcons (*Falco femoralis*) in southern Texas and northern Mexico, and was over twice as successful as hunting (82% versus 37%). Aplomado Falcons pirated prey cooperatively as well as individually. Eight bird species were targeted for piracy, six of which were as large or larger than the falcons. The majority of prey items stolen were mammals. *Received 10 December 2002, accepted 12 March 2003.*

Piracy (kleptoparasitism) has been documented for many birds, particularly those living in open landscapes (Paulson 1985) and has been reported for 12 of 39 species of falcons (Cade 1982, Brockmann and Barnard 1979, Clark et al. 1990, Clark and Schmitt 1993). Hector (1985) observed Aplomado Falcons (*Falco femoralis*) taking small mammals from American Kestrels (*F. sparverius*) and White-tailed Kites (*Elanus leucurus*), and Clark et al. (1990) described piracy by this species on a Little Blue Heron (*Egretta caerulea*). The objective of this study was to determine if piracy is an important foraging mode for both individuals and pairs of Aplomado Falcons in southern Texas and northern Mexico.

We monitored two populations of Aplomado Falcons in southern Texas: one near the Laguna Atascosa National Wildlife Refuge in Cameron County (26° 05′ N, 97° 21′ W) and the other at Matagorda Island National Wildlife Refuge (28° 14′ N, 96° 37′ W). We also observed Aplomado Falcons in the Mexican state of Tamaulipas near the city of Matamoros (25° 49′ N, 97° 26′ W). Most or all individuals were derived from captive stock as part of a long term release program of The Peregrine Fund (Mutch et al. 2000). We observed the activities of breeding pairs during February to June, 1999 to 2002. These pairs occurred in open coastal plains, characterized by low herbaceous cover and few, widely scattered trees and shrubs (Perez et al. 1996). Here we report only piracy and hunting attempts upon vertebrates with known outcomes.

Of 125 foraging forays for vertebrates, 17 (14%) were attempts at piracy, 14 (82%) of which were successful. The hunting success

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←

FRONTISPIECE. Aplomado Falcon (*Falco femoralis*) in southern Texas. Watercolor on paper, by Barry Kent MacKay.

rate was 38% (41 of 108 attempts). This is similar to 37% (n = 100) reported by Hector (1986) for eastern Mexico. Piracy thus was more than twice as successful as hunting.

Although mammals have been included in qualitative accounts of the Aplomado Falcon's diet (Bendire 1892, Cherrie 1916, Bent 1938, Wetmore 1965), recent detailed studies of captured prey and prey remains show no evidence that mammals normally are an important food (only 1 of 341 vertebrate prey items; Hector 1985, Jiménez 1993). Only 2 of the 108 hunts we observed were for mammals, even though we saw Aplomado Falcons consuming mammalian prey of unknown acquisition. However, the majority of identified pirated items were mammals (9 of 13 items of known class; see Hector 1985), suggesting that piracy may account for this incongruity.

Eight (73%) of 11 observed piracy attempts by single falcons were successful, whereas all six attempts by pairs succeeded. These observations parallel the findings of Hector (1986) that pairs were more successful at hunting birds than individuals hunting alone. Our observations imply that piracy by pairs is a cooperative act, involving mutual monitoring of movements and food sharing (Hector 1981, 1986). Four successful piracies by single falcons were in the presence of a nearby mate, whose visibility may have increased the degree of intimidation of the target.

Aplomado Falcons targeted eight species for piracy: the American Kestrel (n = 1), Merlin (*F. columbarius*; n = 1), Peregrine Falcon (*F. peregrinus*; n = 1), White-tailed Kite (n = 6), Northern Harrier (*Circus cyaneus*; n = 3), Chihuahuan Raven (*Corvus cryptoleucus*; n = 2), a gull (most likely Laughing Gull, *Larus atricilla*; n = 1), and other Aplomado Falcons (n = 2). We commonly observed target species in Aplomado Falcon breeding habitat, and White-tailed Kites, the most frequent target for piracy, often nested within sight of Aplomado Falcon nests. Only two of these species, American Kestrels and Merlins, are smaller than Aplomado Falcons (approximately 250–400 g), whereas the others are similar in size or larger (Dunning 1984, Hector 1986). Aplomado Falcons relied on both their impressive flying skills and cooperative attacks to compensate for their lack of size.

Piracy by pairs typically was in the form of a coordinated attack, with the falcons alternately stooping at the target bird, the latter visibly disoriented, vocalizing, and often dropping its prey. In two piracies on Chihuahuan Ravens, the ravens dropped their prey at the first sign of attack, suggesting routine harassment and habituation to surrender. JLB watched a pair of Aplomado Falcons approach a flying White-tailed Kite 5 m above the ground and perform a series of alternating stoops and horizontal attacks. The falcon pair effectively stopped the kite's forward movement, and within 5 s the kite flipped upside down in response to a stoop from the male falcon. The male seized the rodent prey still clutched in the kite's talons, then immediately dropped the prey, which the female falcon caught in mid-air.

Pairs of Aplomado Falcons defending a breeding territory also dominated larger species. Aplomado Falcons attacked and successfully expelled much larger raptors, including Turkey Vultures (*Cathartes aura*), Harris' Hawks (*Parabuteo unicinctus*), White-tailed Hawks (*Buteo albicaudatus*), Red-tailed Hawks (*B. jamaicensis*), Crested Caracaras (*Caracara plancus*), Peregrine Falcons, and Great Horned Owls (*Bubo virginianus*; The Peregrine Fund unpubl. data). In contrast, nonbreeding Aplomado Falcons tended to tolerate heterospecific intruders. Temeles (1990) suggested that such behavior by Northern Harriers increased opportunity for kleptoparasitism by not excluding potential future targets. Our observations indicate that Aplomado Falcons, particularly when paired, may improve their foraging efficiency and broaden their diet by pirating.

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DESCRIPTION OF THE NEST, EGGS, AND BREEDING BEHAVIOR OF THE ENDANGERED PALE-HEADED BRUSH-FINCH (*ATLAPETES PALLIDICEPS*) IN ECUADOR

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ABSTRACT.—The Pale-headed Brush-Finch (*Atlapetes pallidiceps*) is a critically endangered endemic bird species that is restricted to a single valley in southern Ecuador. We present the first description of the nest, eggs, breeding behavior, and juvenal plumage of this species. Seventy-two percent of nests (n = 18) were placed on thin overhanging branches 1–3 m above the ground, directly beneath the top layer of foliage in dense thickets. Nesting material consisted of various proportions of grass, twigs, and bamboo stalks and leaves. Clutch sizes ranged from 1–3 eggs (n = 22), and ≥55% of nests (n = 18) were parasitized by Shiny Cowbirds (*Molothrus bonariensis*). The background color of eggs was buffish white to bluish, and they were spotted and blotched with diffuse brown markings. Mean egg size was 24 × 17.8 mm. Fledgling plumage differed from adult plumage and had some characteristics similar to the adult White-winged Brush-Finch (*Atlapetes leucopterus*). Females alone incubated the eggs, and both parents fed the offspring. Incubation and nestling times were 12–14 days each. Fledglings of the Pale-headed Brush-Finch were led for several weeks after fledging. No pair initiated a second clutch after a successful first one (n = 16), but we observed second and third clutches after nest failure had occurred. Prolonged postfledging care is assumed to prevent multiple broods of the Pale-headed Brush-Finch during one season. *Received 13 February 2003, accepted 30 July 2003.*

The avian genus *Atlapetes* (Aves: Emberizidae) comprises more than 20 species of brush-finches, which inhabit dense forest undergrowth, forest edge, or shrubby nonforest habitats in Central America and the Andes of South America (Paynter 1972, 1978; Hilty and Brown 1986; Ridgely and Greenfield 2001). Geographic differentiation and species limits are highly complex in the genus and have been revised recently (Remsen and Graves 1995, Garcia-Moreno and Fjeldså 1999). At least seven *Atlapetes* species have a restricted geographic range (Paynter 1978, Valqui and Fjeldså 1999). One of these is the Pale-headed Brush-Finch (*Atlapetes pallidiceps*), a critically endangered endemic that is limited to the upper Rio Jubones valley system of the Azuay province in southern Ecuador (Paynter 1972, Collar et al. 1992, BirdLife International 2000). The species was rediscovered in the Yunguilla Valley in 1998, after being unrecorded for 30 years (Agreda et al. 1999). Breeding behavior and nesting have not been described previously.

The only currently known population of *A. pallidiceps* consists of approximately 35 pairs which inhabit dense secondary scrub above a semiarid inter-Andean valley (N. Krabbe unpubl. data). The area is inhabited and intensively farmed, and due to ongoing clearance of forest for the creation of pastures, it is largely devoid of forest tracts (Bossuyt et al. 1997). Land use-induced loss of habitat is presumed to pose a serious threat to the remnant population (Agreda et al. 1999). In this study, we investigated the breeding biology and nesting requirements of the Pale-headed Brush-Finch in order to identify the main threats to its population and derive management objectives for its future conservation.

STUDY AREA AND METHODS

The study area was located in Yunguilla Valley, approximately 50 km southwest of Cuenca in the upper Rio Jubones drainage, Province Azuay, Ecuador (03° 13′ S, 79° 16′ W). It encompassed three steep (about 45°) slopes with an area of 50 ha ranging from 1,650–2,000 m in elevation. The site with the greatest concentration of brush-finch territories has been declared a reserve and is largely ungrazed, whereas a population on the neighboring hill inhabits an area that is still grazed

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by cattle (Agreda et al. 1999). Both hills feature semi-open habitats with dense arid scrub consisting mostly of composite and verbenaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* sp. and lauraceous trees are found in more humid parts, and fragments of semihumid forest persist on western and southern slopes. Monocultural stands of *Chusquea* sp. bamboo form large patches of habitat in small depressions, ravines, or on the western slopes. The arid scrub is deciduous and sheds its leaves during the dry season from June to December, whereas the bamboo remains green all year.

We monitored birds from mid-March to mid-July 2002 every morning between 05:45 and 08:45 (EST), when singing activity was most prominent. We mapped territories by connecting all song perches of a male to a minimum convex polygon, and tried to adjust territory boundaries based on further observations of intraspecific interactions and response to song playbacks. We searched for nests in the center among the males' most frequently used song perches, and located them by following birds returning to the nest (Martin and Geupel 1993). In order to minimize disturbance, we did not approach active nests closer than 3 m unless both parents were absent. We judged nest stage (incubation or nestling) from parental behavior and monitored nest stage every 3–5 days. After fledging or nest failure had occurred, we measured any remaining eggs and the nest and recorded the following variables: egg length, width, and coloration; nest height above ground; nest diameter; depth of nest cup; nest circumference; nesting material; and nest cover. Length variables were measured with a flexible tape measure, components of nest composition (material) were estimated to the nearest 10%, and cover was estimated by the percentage of nest shading at noon on a sunny day. We tried to determine causes of nest failure by searching the nest vicinity for signs of predators or remnants of eggs, chicks, or nesting material.

We confined our observations of breeding behavior to four nest sites that offered good viewing conditions without causing distress to the birds. In order to record parental movements, we observed nest sites for two consecutive hours during incubation, and for up to four consecutive hours during the nestling stage. We judged diet composition mainly from food carried to the nest, and from occasional foraging observations where the prey item could be determined. We recorded foraging behavior on an opportunistic basis whenever birds were followed.

FIG. 1. Nest and eggs of the Pale-headed Brush-Finch (*Atlapetes pallidiceps*) from Yunguilla Valley, Ecuador, April 2003. Photograph by H. Martin Schaefer.

In 2003, we monitored birds between late February and late May, and used these additional observations to support findings of the 2002 season. We did not measure nests and eggs in 2003, and all reported sample sizes refer to 2002 data unless otherwise stated.

RESULTS

Nests.—We found 18 nests of 13 different pairs of Pale-headed Brush-Finches. Renesting occurred in five pairs, of which two pairs renested twice and built three nests altogether. Distances between consecutive nests of one pair ranged from 15–45 m. Thirteen nests (72%) were attached to thin (<1 cm diameter) overhanging branches of shrubs or vines, and 11 of these were just beneath the top layer of the foliage. We found five nests in forks or along the main stem of erect standing bushes within tall stands of grass. Mean height above ground was 184 cm ± 61 SD (range, 84–302 cm). All but two nests were located on slopes exceeding 30°, the general inclination at the study site. The nest was a bulky open cup, constructed of small twigs, grass straws, herbaceous stems, or bamboo stalks (Fig. 1). Moss and lichen also were present in the nest, but only in small quantities comprising <5% of the nesting material. Depending upon surrounding vegetation, material composition varied from almost entirely (90%) bamboo

with a few twigs, to 70% grass, with twigs and stems but no bamboo. Nest cups were lined with fine grass, leaf fibers or bamboo leaves. Mean outer nest diameter was 127 mm ± 13 SD (range, 100–150 mm), and mean cup diameter was 69 mm ± 9 SD (range, 50–85 mm). Mean cup depth was 50 mm ± 5 SD (range, 45–60 mm), and mean nest cup circumference was 385 mm ± 64 (range, 245–510 mm). Nests had a mean foliage cover of 75% (range, 50–100%).

Eggs.—The eggs were subelliptical to oval in shape. Background color varied from buffish white to light bluish or a faint rosy pink, and eggs were of intermediate gloss (Fig. 1). Markings were deeply ingrained into the shell. They formed irregularly shaped spots without clear cut outlines, and ranged from very light to dark brown in color. Small markings were distributed over the entire surface, and often accumulated to large continuous spots around the poles. A large number of pinpoint-sized spots and speckles of blackish purple color were randomly distributed across the entire shell. For nine eggs, mean length was 24.0 mm ± 0.7 SD (range, 23–25 mm) and mean width was 17.8 mm ± 0.5 SD (range, 17–18 mm). Pale-headed Brush-Finch eggs differed slightly from the eggs of the Shiny Cowbird (*Molothrus bonariensis*), which were pale bluish, less glossy, with few dark purple spots, and with indistinct spots on the poles ($n = 6$).

During 2002, we inspected seven nests during the incubation stage, of which six contained two eggs each, and one contained three eggs. We found 1–3 parasitic cowbird eggs in five of the seven nests. This complicated assessment of mean clutch size, because cowbirds are known to remove host eggs when laying their own (Wood and Bollinger 1997, McLaren and Sealy 2000, Granfors et al. 2001). During 2003, we found 10 clutches containing one ($n = 4$), two ($n = 5$) or three ($n = 1$) eggs. Due to cowbird control in 2003, numbers of parasitic eggs were not comparable to the 2002 season.

Juveniles.—Plumage of nestlings was mostly uniform brown (Fig. 2). Tail, wing, and ventral coloration of the fledged offspring of the Pale-headed Brush-Finch was almost identical to the adult plumage, but the head pattern was strikingly different ($n = 9$). It was mostly slaty gray with a prominent dark rufous to rusty brown crown stripe extending from the top of the head down to the nape. Facial pattern was uniform, with an indistinct narrow black malar stripe. An off white to light gray ear patch developed about 2–3 weeks after fledging. The forehead also was dull gray, and showed two small buffy white supraloral spots. The beak was dull yellowish horn in color with a black culmen, and became gradually darker with increasing age. Slaty gray forehead with off white supraloral spots and a rusty brown crown stripe were characteristics similar to those in the southern White-winged Brush-Finch (*Atlapetes leucopterus dresseri*). The slaty color of the head extended to below the chin and was demarcated by an off white to buffish collar. Chest, belly, and underparts were buffish gray, and provided a well delineated contrast to the lighter collar. Flanks were slightly streaked gray, and thus darker than the midbelly. The rusty brown

FIG. 2. Nestling of the Pale-headed Brush-Finch (*Atlapetes pallidiceps*) in Yunguilla Valley, Ecuador, April 2003. Photograph by H. Martin Schaefer.

crown stripe merged without contrast into the brown back, which differed markedly from the darker gray-brown wings. The extent of the crown stripe appeared to diminish with increasing age of the juveniles. Simultaneously, the auricular patch developed stronger, giving the bird a blotchy appearance. Four adult birds were noted to have very broad brown facial markings, while three other adults had almost entirely white heads.

Breeding behavior.—Breeding activity commenced in February and nesting continued until late June. First clutches were initiated between February and April, and we confirmed this asynchronized breeding in 2003, with first clutches being laid between early February and early April. Singing activity was most prominent during early morning, and continued only until midday in very humid conditions (during fog or drizzle). Intensity and frequency of songs varied greatly among pairs, but generally declined during incubation and was reduced to almost zero at the nestling stage and while leading fledglings. Singing was elicited by the use of playbacks in only 2% of all attempts, and even neighboring males that intruded into a given territory did not necessarily elicit a response by the territory owner. Territorial defense was weak in that we observed agitated countersinging in only 2 of 27 cases where a male or a pair crossed the line of song perches frequently used by its neighbor. Territory boundaries were therefore rather ambiguous. Areas adjacent to different territories often were used by different pairs for foraging and singing at different times. We did not observe any aggressive interactions between conspecifics, or between the Pale-headed Brush-Finch and the sympatric Stripe-headed Brush-Finch (*Buarremon torquatus*).

Territory size ranged from approximately 0.5–2.0 hectares, and varied throughout the season. Neighboring pairs extended their home range or territories to occupy a vacant lot in places where another pair had abandoned its territory after a failed nesting attempt ($n = 2$). Five pairs ventured into previously unvisited neighboring areas while leading fledglings, regardless of these areas being occupied by conspecifics or not.

The female alone appeared to build the nest and incubate the eggs, and both parents fed the offspring. No incubation feeding was observed. During incubation, the male approached the nest in regular intervals to call the female off, and both foraged together for approximately 15–20 min. The female returned alone and remained in dense cover and very close to the ground while approaching the nest. During the nestling stage, the parents foraged independently and returned to the nest to feed the offspring every 5–25 min, depending upon age and size of the chicks. Food items that we could identify included invertebrates such as crickets and grasshoppers (Orthoptera), caterpillars (Lepidoptera larvae), adult Lepidoptera, beetles (Coleoptera), and earthworms (Lumbricidae). More than half of the food items we observed were fairly large, ranging from 1–3 cm in length. We observed a fruit being fed to nestlings only once, although we regularly observed adults eating fruit (*Rubus* sp.).

We found 61% of nests during the nestling stage, therefore only limited information is available regarding incubation length and fledging age of chicks. However, in three instances, where we observed the female building the nest, we observed the pair with fledglings 32–35 days later, indicating that incubation and nestling stages were approximately 12–14 days each. This was confirmed in 2003, when we documented 14 days between laying and hatching ($n = 2$), and 11.5 days between hatching and fledging ($n = 2$).

The first chicks fledged in late March and the last chicks fledged in late June. The offspring remained stationary inside very dense thickets for the first few days after fledging. Surviving fledglings were fed by their parents for ≥4 weeks, and three families stayed together for ≥8 weeks. We did not observe any pair leading more than two fledglings. Fledglings were able to forage independently after 3–4 weeks, but they still accepted food delivered by their parents.

In four nests that were parasitized by Shiny Cowbirds, only one cowbird fledgling was raised, but we also observed two mixed broods (one cowbird, one brush-finch fledgling) and one clutch with two cowbird fledglings. Brood parasitism affected almost half the population and presently is regarded to be the main threat to the Pale-headed Brush-Finch (SO unpubl. data). Otherwise failed

nests were either depredated (n = 5 in 2003) or abandoned (n = 4 in 2003). In one case, the nest was abandoned after a cow had destroyed the nesting bush.

Renesting occurred 1–3 weeks after we noticed breeding failure. At least two pairs initiated three nesting attempts after the first two had been unsuccessful. We observed no pair that started renesting after a successful brood (n = 16 for both years combined). Two pairs that fledged their first clutch in early April did not attempt a second brood. Altogether, timing and number of clutches was highly variable among pairs. In two pairs we could not discover any signs of nesting activity despite equal observation effort.

Foraging behavior.—We observed foraging mainly in scrub, and only rarely (<1% of time) in open grassy habitat or in taller trees. Foraging heights ranged from 0–4 m above the ground, with medium heights (2–3 m) most frequently observed. Most prey items were gleaned from the foliage or small twigs while the bird was perched, but we also noted short sallying, hovering, and flycatching. Birds also ripped and searched through debris and dead leaves on the ground and removed prey items from the soil. We observed three individuals pick at inflorescences of larger bushes. Blackberries (*Rubus* sp.) were consumed regularly, and two individuals fed on grass seeds that could be reached from a low perch branch.

We observed birds foraging in bamboo on only three occasions, even though bamboo scrub covered up to 75% of some territories and was used for nest sites. If foraging occurred in bamboo, it was at ground level; we did not observe foliage gleaning in bamboo.

DISCUSSION

The Pale-headed Brush-Finch occurs in a narrow climatic transitional zone with distinct seasonal rainfall distribution (Paynter 1972, Bossuyt et al. 1997). Breeding appears to be closely linked to the rainy season in the area, as also has been noted for other brush-finches (Koepcke 1958, Paynter 1972). The onset of the rainy season often triggers increases in insect abundance, which might be required to compensate for elevated energetic requirements (Aguilar et al. 2000).

Foraging appeared to be unspecialized and we recorded a large number of different prey items. Insects and larvae were used most frequently, but grass seeds and flower buds also were consumed. Paynter (1972) analyzed the stomach contents of eight Pale-headed Brush-Finches and found insect remains and cracked seeds along with large quantities of sand. The dominance of invertebrate prey observed during this study might be due to seasonal variation in food availability and consumption, as the gut analysis was conducted in November (Paynter 1972). Like most feeding generalists, other *Atlapetes* species also have been noted to be insectivorous during the breeding season (Paynter 1978).

That we did not observe Pale-headed Brush-Finches forage in bamboo scrub might be due to the monostructural composition of bamboo stands. Lower diversity in plant species and structure typically support lower numbers of invertebrates (Rotenberry and Wiens 1998, Söderström et al. 2001), which might render bamboo an inefficient foraging substrate for an unspecialized bird. On the other hand, bamboo is very dense and obstructs visual observations, which might have led to the false assumption that it is rarely used for foraging.

All but two nest sites were on steep slopes, and 72% of nests were found on high drooping branches or vines that extended away from the main stem. This has not been described for other *Atlapetes* species (Pereyra 1951, Paynter 1978, Greeney et al. 1998, Salaman et al. 1998). The construction of nests on very thin branches or vines may restrict access by some mammalian predators (e.g., mustelids), which are too heavy to be supported by the small branches. The availability of overhanging vines and bamboo stalks as nesting habitat might contribute to the restricted distribution of the Pale-headed Brush-Finch.

The nest structure and composition of the Pale-headed Brush-Finch is consistent with the descriptions of nests of other brush-finch species, which generally are described as open cups of straws, weeds, and grass, positioned in dense tangles close to the ground (Pereyra 1951, Paynter 1978, Hilty and Brown 1986, Greeney et al. 1998, DiGiacomo and Lopez-Lanús 2000) or higher up in trees (Salaman et al. 1998). Nesting material generally is taken from the surroundings (within 20–30 m) and

varies according to the local vegetation. The Pale-headed Brush-Finch appears to be a generalist in its selection of nesting material, using the most common materials available in its respective territory.

Egg measurements of *A. pallidiceps* were similar to those of other *Atlapetes* species described in the literature, ranging from 20.9 × 15.9 mm (*A. pileatus*; Schönwetter 1984) to 27.5 × 18.5 mm (*A. leucopis*; Salaman et al. 1998). Egg color in the brush-finches is either bluish with very few or no spots (Rowley 1962, Paynter 1978, Hilty and Brown 1986, Greeney et al. 1998), or pale cream with chestnut blotches (Schönwetter 1984, Salaman et al. 1998). *A. pallidiceps* eggs are intermediate between both descriptions. The less glossy eggs with fewer spots found in this study were ascribed to be of parasitic origin. The Shiny Cowbird has been recorded to have different egg colorations, including a spotted bluish morph of 25.4 × 20.3 mm in size (Schönwetter 1984, Johnsgard 1997, Fraga 2002). The eggs of both species show considerable overlap in size and background color, and further research is required to identify characteristics unique to the eggs of one species.

The Pale-headed Brush-Finch produces clutches of 1–3 eggs, as generally found in tropical passerine birds. Relatively small clutch sizes have been hypothesized to be a result of increased adult survival and reduced reproductive effort (Martin et al. 2000). There was no evidence of a second breeding attempt following successful breeding earlier in the season. Double brooding may be impossible given the prolonged period of postfledging parental care. In one case, a second breeding attempt followed an apparently successful attempt, but the second clutch was initiated only 13 days after the first chicks left the nest, which strongly suggests that the fledglings died. This re-lay interval was typical of that following breeding failure. Second and third clutches were initiated only when the previous clutches had failed.

Agreda et al. (1999) and Ridgely and Greenfield (2001) stated that pairs of the Pale-headed Brush-Finch usually forage together, which is common in several species of the genus (Paynter 1978, Lopez-Lanús et al. 2000). During the incubation stage, females were guarded by their mates when they left the nest to forage. Both during the nestling stage and while feeding fledglings, partners often foraged alone. Birds foraging by themselves did not utter contact calls, making them much harder to detect. We conclude that joint foraging is no more pronounced than solitary movements during the breeding season.

Agreda et al. (1999) found that tape playbacks yielded only a weak response in the Pale-headed Brush-Finch. This is consistent with the results of this study, where we observed almost no response to playbacks, and where territorial defense to conspecific intruders was entirely absent at times. While the biological reason for the lack of territorial defense needs to be analyzed in more detail, this behavior is of crucial importance for the assessment of distribution and population size. During previous searches, lack of singing activity has been taken as circumstantial evidence that the species was absent (Collar et al. 1992). Given the low singing intensities and the lack of response to playbacks even from breeding birds, care needs to be taken when declaring an area to be without the Pale-headed Brush-Finch.

N. Krabbe (pers. comm.) pointed out that small tract sizes of remaining suitable habitat might have led to the local extinction of the Pale-headed Brush-Finch. This study has identified nesting habitat as a new potential requirement that previously defined suitable habitat might lack. Detailed analysis of habitat selection will soon be available (Oppel et al. in press), but further ecological investigations into dispersal abilities, breeding biology, and population threats would be an important step aiding future recovery of the Pale-headed Brush-Finch.

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THE NEST, NESTING BEHAVIOR, AND FORAGING ECOLOGY OF THE RUSTY-WINGED BARBTAIL (*PREMNORNIS GUTTULIGERA*)

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ABSTRACT.—We discovered and monitored a nest of the Rusty-winged Barbtail (*Premnornis guttuligera*) on the eastern slope of the Andes in Napo Province, Ecuador. The nest, in a hollow *Cyathea* tree-fern snag, was a deep cup composed entirely of *Cyathea* tree-fern petiole scales (ramenta). A single nestling fledged successfully on 13 March 2002. During the latter half of the nestling period, adults visited the nest with food a mean of 4.7 ± 1.9 (SD) times/h and removed fecal sacs 2.2 ± 1.1 times/h. Nest visitation rates generally decreased throughout the day. Adult Rusty-winged Barbtails foraged by gleaning from or probing into suspended dead leaves or moss, often while hanging onto the substrate, and did not hitch up trunks or creep along branches. Nest structure, composition, and location, and foraging behavior all raise doubts about the taxonomic placement of *Premnornis* in the *Margarornis* treerunner-barbtail assemblage. *Received 18 March 2003, accepted 25 June 2003.*

The Rusty-winged Barbtail (*Premnornis guttuligera*) is an uncommon and poorly known Neotropical ovenbird (Furnariidae) that inhabits lower growth of montane forest from western Venezuela to southern Peru (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Remsen 2003). In Ecuador, the species is locally distributed in the subtropical zone, primarily between 1,600 and 2,300 m on the eastern slope of the Andes (Ridgely and Greenfield 2001). Little has been published on the natural history of the Rusty-winged Barbtail, and virtually nothing is known of its breeding biology (Remsen 2003).

Based on general morphology (e.g., size, wing shape, tarsus:toe length ratio, plumage coloration and pattern) and hindlimb musculature, the Rusty-winged Barbtail appears to be most closely related to *Premnoplex* and *Roraimia* barbtails and *Margarornis* treerunners, collectively known as the *Margarornis* assemblage (Vaurie 1980; Rudge and Raikow 1992a, 1992b). Ecologically and behaviorally, however, the Rusty-winged Barbtail differs strongly from those species, some of which (i.e., *Margarornis*; little data exists for *Premnoplex* and *Roraimia*) typically forage by hitching up tree trunks and along branches in a manner similar to woodcreepers (Dendrocolaptidae) and creepers (Certhiidae). In contrast, Rusty-winged Barbtails forage by moving along branches and through dense vegetation (e.g., vine tangles) and probing dead leaves and moss, much like many foliage-gleaners and some *Cranioleuca* spinetails (Miller 1963, Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Ridgely and Greenfield 2001). Despite the common assumption that the Rusty-winged Barbtail shares scansorial (tree climbing) habits with other species of the *Margarornis* assemblage (Wetmore 1972; Vaurie 1980; Rudge and Raikow 1992a, 1992b), this is not the case (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, authors pers. obs.).

Nest structure and placement represent behavioral traits that have proven informative in reconstructing phylogenetic relationships within Furnariidae (Zyskowski and Prum 1999). *Premnoplex* barbtails and *Margarornis* treerunners exhibit similar nest architecture and nest placement; species in both genera build mossy, globular nests, placed beneath logs, against banks, or are suspended from vegetation (Hilty and Brown 1986, Ridgely and Tudor 1994, authors pers. obs.). Thus, morphological, ecological, and behavioral characteristics are consistent in suggesting that *Premnoplex* and *Margarornis* are very closely related (Rudge and Raikow 1992b, Zyskowski and Prum 1999). Information of nest structure and placement of the Rusty-winged Barbtail may yield important insights into the species' phylogenetic relationships and, hence, how to interpret the morphological, ecological, and behavioral differences be-

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tween *Premnornis* and virtually all other species of the *Margarornis* assemblage. Here we provide the first description of a nest and nest site of the Rusty-winged Barbtail, as well as details on nestling appearance, parental care, and adult foraging behavior.

METHODS

We observed a Rusty-winged Barbtail nest during February and March 2002 in primary montane evergreen forest at 2,100 m on the eastern slope of the Andes, near Yanayacu Biological Station (00° 36′ S, 77° 54′ W), about 3 km southwest of Cosanga, Napo Province, Ecuador. This humid "cloud" forest is characterized by heavy epiphytic growth, a canopy 20–25 m in height, and gently rolling topography. We based species identification on a combination of plumage pattern (scalloped breast pattern, lack of bold back streaking), morphology (thin bill and decurved culmen), and high-pitched, thin vocalizations, which separate the species from all other sympatric furnariids.

We documented nestling appearance on 28 February, and again on 3 March when we also recorded nestling mass and linear measurements. To access the nest, which was in a tree cavity (see below), we cut away a panel of bark at the level of the nest. We used mud the same color as the bark to cement the panel of bark back into its original position. This disturbance did not appear to affect the adult birds, which apparently remained absent during our presence at the nest and resumed normal activity soon after our departure from the immediate area. We measured nest dimensions on 3 March and immediately following fledging on 14 March, when we removed the nest from the cavity for examination.

We observed and quantified adult behavior at the nest during three 3-h periods per day (07:00–10:00, 11:00–14:00, 15:00–18:00 EST), every other day from 2 to 12 March, for a total of 54 h of observation comprising the majority of six days. We conducted an additional 7.9 h of observation at other times (e.g., at dusk to determine roosting activity). We conducted nest watches from a concealed position in the understory, 20 m away from the nest site. The observer's presence did not appear to affect the birds' behavior. Quantified behaviors included nest visitation rate, method of nest approach and entrance, time present inside and outside the nest, and fecal sac removal rate. We also described less common behaviors and activity patterns (e.g., nest defense, adult interactions, roosting behavior).

We also collected data opportunistically on Rusty-winged Barbtail foraging behavior. Between 17 March and 11 April 2002, and on 5 February 2003, we followed and observed adults of unknown breeding status as we encountered them in the forest. While observing a foraging individual, we dictated its actions into a microcassette recorder. For each prey attack, we noted the bird's height, distance to canopy, type of attack maneuver, and prey substrate (following Remsen and Robinson 1990). For analysis of height variables, we included only data from the first attack observed for a given bird.

RESULTS

Nest discovery and phenology.—We discovered the nest on 22 February 2002 by observing adults taking food into the nest cavity. Adults visiting the nest with food always remained within the cavity for 5–25 min, and often left with fecal material. On 22 February, adults spent approximately 80% of three observation hours inside the cavity, apparently brooding young. A single nestling showed little development and was largely naked when examined on 28 February. The nestling fledged on 13 March before 14:50.

Nest site and habitat.—The nest was in a 4.53-m tall, dead (standing) *Cyathea* tree-fern stump. Three openings in the bark allowed access to the completely hollow interior of the snag. One opening was a slender, natural crack in the bark that measured 19.5 × 4.0 cm, faced a 30° orientation, and was near the top of the snag, 4.08 m above the ground. Two other holes in the bark were rectangular in shape, with rough and irregular edges, and appeared to have been made by a bird. The larger of these, which was the entrance most often used by the birds, measured 3.0 × 5.5 cm, had an 80° orientation, and was located 3.44 m above the ground. The third and least-used entrance measured 2.0 × 3.7 cm and was approximately the same height as the main entrance hole, but on the opposite side of the snag, facing 210°.

The nest site was midway up a drainage

slope, about 30 m from a small stream, inside primary forest. Canopy height was about 20 m. Live tree-ferns and mid-sized trees formed a subcanopy 8–10 m in height above the nest site. The understory was relatively thick with 1- to 2-m tall saplings and ferns. Two live, 8- to 9-m tall tree-ferns were located <3 m of the nest snag; the next closest tree was 7 m away from the nest site.

Nest description.—The nest was an open cup (Fig. 1), the rim of which was located 2.82 m above the ground and 62 cm below the main entrance hole. Nest material filled the entire cylinder of the hollow snag for 22.5 cm vertically, from the rim of the cup to the bottom exterior of the nest. Material at the bottom of the nest did not rest on the bottom of a cavity, but was supported by thin strands of bark that had peeled away from the inner walls of the snag. The nest, however, appeared to be supported primarily by the bulk of the material itself, which was packed into the cavity such that outward pressure against the walls of the snag provided support. The outer diameter of the cup, equivalent to the inner diameter of the snag, measured 12.4 cm. The inner diameter of the cup, which did not change in size or shape from early to late in the nestling period, measured 6.6 cm. The inner depth of the cup changed dramatically as the nestling grew. Early in the nestling period (28 February), cup depth was 7.9 cm, which resulted in a very narrow, deep, and almost cone-shaped inner cup. By fledging (14 March), cup depth was only 3.2 cm, resulting in a shallow cup.

The nest consisted completely of *Cyathea* tree-fern petiole scales (ramenta), which are thin, soft, and flexible. No distinct lining was placed in the bottom of the cup.

Nestling description.—We documented the appearance and took measurements of the nestling on 3 March, an estimated 9–11 days after hatching and 10 days before fledging. At 12:00, the primary pin feathers were exposed 1.5 mm from their sheaths and the nestling weighed 16.2 g. Tarsus length was 18.6 mm, wing chord was 29.3 mm, culmen length was 10.2 mm, and gape width was 14.2 mm. Although capable of opening its eyes slightly while begging, the nestling generally kept its eyes closed. Skin on the body was pinkish with a slight orange tinge. Legs and feet were mauve and the bill was grayish black in color. Flanges of the gape were whitish yellow and the mouth lining was yellowish orange. Pin feathers with gray sheaths were coming in on all feather tracts. Rust-colored pin feathers had broken their sheaths on dorsal and ventral tracts and on wing coverts. Secondary and primary pin feathers had recently broken their sheaths and were grayish brown in color. Sparse downy plumes were present on the head and back.

Nest attendance.—We observed the nest for a total 61.9 h, primarily during the latter half of the nestling period (2–12 March). Adults always carried food (arthropods) in their bills when going to the nest. Adults typically approached the nest through the understory, making a final short flight upward to a cavity entrance, or through a series of incrementally closer flights between trees with a final horizontal flight to a cavity entrance. When approaching or leaving the nest, adults flew directly to or away from a cavity entrance, or within 10 cm of a cavity entrance, rather than creeping up or down the trunk before entering or leaving the cavity. Flights away from the nest typically were long (>20 m) horizontal flights and occasionally were preceded by looking out of the hole (for up to 50 s).

Overall nest visitation rate (mean ± SD) by the adults was 4.7 ± 1.9 nest visits/h (range 1–8; n = 54 h). Among days, mean nest visitation rate ranged from 4.1–5.6 nest visits/h and did not appear to vary with nestling age. Within each day, nest visitation rate tended to decrease throughout the day, with a slight increase late in the afternoon (Fig. 2). An adult arriving to find its mate already inside the nest cavity typically perched outside and waited for its mate to leave before entering the cavity. Both adults were present at the nest site simultaneously during only 3% (7) of 254 nest visits, and both were inside the cavity simultaneously only once. Of the three nest cavity entrances, the adults clearly favored the larger rectangular hole, using it for 96% of 424 nest cavity entrance and exit events.

Time spent inside the nest cavity by adults, presumably brooding, did not show a consistent pattern throughout the day. However, time (% of observation time) spent in the cavity appeared to decrease as the nestling grew, from approximately 80% on 22 February to

FIG. 1. Rusty-winged Barbtail nest inside hollow tree-fern snag, with section of bark cut away to show nest structure. Photograph by B. Swift, Napo Province, Ecuador, 14 March 2002.

30% on 2 March, 8% on 4 March, 5% on 6 March, 4% on 8 March, 2% on 10 March, and 3% on 12 March. Mean time spent in the nest cavity per visit declined from 3.3 min on 2 March to 0.3 min on 12 March, whereas maximum duration of time spent in the nest cavity decreased from 15.6 min to 1.1 min over that same period. Adults always entered the nest

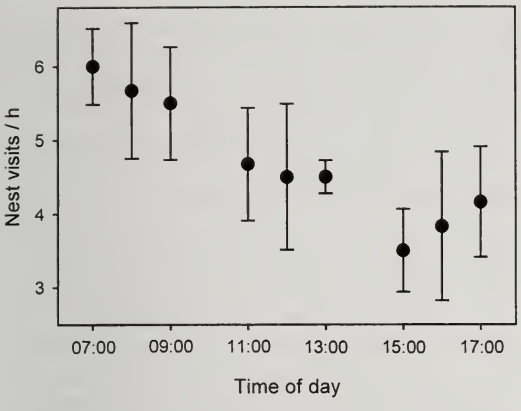

FIG. 2. Diurnal pattern of Rusty-winged Barbtail nest visitation was generally decreasing during the latter half of the nestling period. Symbols represent mean (± SE) number of nest visits/h (n = 54 h, 9 h/day for six days). Data are from Napo Province, Ecuador, 2002.

cavity, spending ≥7 s inside, during nest visits and never were observed feeding the nestling from outside the cavity.

One adult slept inside the nest cavity during the nights of 2, 4, 6, 8, and 10 March, entering the cavity (with food) for the last time between 18:08 and 18:21 (mean = 18:14). The roosting adult had left the nest by 06:45 each morning, and by 06:17 one morning. No adult roosted in the nest cavity the night of 12 March, just prior to fledging (13 March).

Adults removed fecal sacs from the nest after 46% of nest visits (n = 254 nest visits). Overall, adults removed fecal material 2.2 ± 1.1 times/h (range 0–5). There was no consistent pattern in fecal sac removal rate with respect to time of day or nestling age (within the latter half of the nestling period). Adults carried fecal sacs in their bills and flew ≥20 m away from the nest before disposing of them, the exact method of which was not determined.

Nestling begging, audible from a distance of 20 m on 4 March, was a sustained, high-pitched, insect-like vocalization with pulses of emphasis. The nestling typically begged 1–2 s after an adult arrived and entered the cavity and again as it left the cavity, quickly becoming quiet after the adult's departure. The nestling did not beg when an adult perched outside the cavity entrance.

Nest defense.—We observed two nest defense events by adult Rusty-winged Barbtails when woodcreepers (Dendrocolaptidae) perched on the nest snag. On 8 March a Montane Woodcreeper (*Lepidocolaptes lacrymiger*) flew to and perched on the nest snag, 20 cm below the main nest cavity entrance. Within 2 s of the woodcreeper landing on the nest snag, a single adult barbtail flew in, displaced and chased the (larger) woodcreeper >20 m away from the nest site. Nestling provisioning resumed 7 min later.

On 12 March, at 07:54, a Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*) flew to and perched on the nest snag, landing near the main entrance and moving up to the natural hole. Within 5 s both adult barbtails, one carrying food, began diving at the (much larger) woodcreeper, making 10–12 dives during 20 s, at which time the woodcreeper flew away. Neither adult barbtail appeared to hit the woodcreeper, but each approached it closely during each dive and one chased it approximately 10 m as it flew. Both barbtails remained agitated near the nest for 13 min, repeatedly diving over the nest site, flicking wings when perched, and giving emphatic, high-pitched, and slightly downslurred "tsep" alarm calls. One adult made several brief visits to the main cavity entrance, but was immediately displaced and chased by its mate. Both adults left the area at 08:07 and remained absent for 25 min, returning at 08:32. At 08:35, 41 min after the woodcreeper left the nest site, nestling provisioning resumed. Adults remained agitated, giving alarm calls and often flying past the nest site before going to it, until 08:40.

Foraging behavior.—Rusty-winged Barbtails foraged with mixed-species flocks, primarily in vine tangles and among mossy branches and live foliage, from the understory to the subcanopy. Mean foraging height was 6.6 ± 3.5 m (range 1.8–10.7; n = 6); mean distance to canopy was 11.9 ± 4.7 m (range 6.1–16.8). Rusty-winged Barbtails gleaned arthropods from surfaces and probed into crevices of substrates, often while hanging-up (i.e., clinging to a substrate in a vertical, head-up position) or hanging-sideways (i.e., hanging in a horizontal posture; see Remsen and Robinson 1990) on a moss-covered branch or large dead leaf (e.g., *Cecropia* sp.). Rusty-winged Barbtails frequently hopped and made

short flights between perches while searching for prey, and did not hitch up vertical branches or trunks in the manner that both Spotted Barbtails (*Premnoplex brunnescens*) and Pearled Treerunners (*Margarornis squamiger*) frequently do (RCD pers. obs.). The Rusty-winged Barbtail appears to be a regular dead leaf forager (*sensu* Remsen and Parker 1984), with 53% of attacks directed at prey in or on suspended dead leaves, which ranged from 3 × 5 cm to 40 × 40 cm in size. Other prey substrates included small, dead or live moss-covered branches (37%), suspended moss (3%), vine stems (3%), and live leaves (4%; $n = 30$ attacks by six birds). Rusty-winged Barbtails typically searched small (e.g., 1- to 5-cm diameter) moss-covered branches.

DISCUSSION

The Rusty-winged Barbtail nest described here was active in February and March, and probably as early as late January, which is consistent with timing of breeding evidence recorded elsewhere in the northern Andes. Fledglings have been observed in January and February in northeastern Ecuador and during January in the western Andes of Colombia (Fjeldså and Krabbe 1990); adults in breeding condition have been collected during March in the western Andes of Colombia (Miller 1963). Records of fledglings in northeastern, northwestern, and southern Ecuador (Fjeldså and Krabbe 1990) indicate that the species also breeds from September to November on the eastern slope of the Ecuadorian Andes.

The nest of the Rusty-winged Barbtail was a cup composed of tree-fern petiole scales, built in the hollow column of a tree-fern snag. Thus, nest structure, composition, and placement set *Premnornis* apart from its allies, *Premnoplex* barbtails and *Margarornis* treerunners, which use mosses and liverworts to construct globular nests with side or bottom entrance holes, placed against banks, under logs, or in suspended vegetation (Skutch 1967, Vaurie 1980, Hilty and Brown 1986, Fjeldså and Krabbe 1990, Marín and Carrión 1994). In contrast, the Rusty-winged Barbtail is similar to several other furnariid taxa, also in the subfamily Philydorinae, with respect to nest structure and placement. *Anabazenops*, some *Philydor*, and at least two species of *Syndactyla* foliage-gleaners build cup-shaped nests with pliable materials in tree cavities, as do species of *Xenops* (Skutch 1969, Vaurie 1980, Belton 1984, Hilty and Brown 1986, Kratter 1994, Zyskowski and Prum 1999).

The nest of the Rusty-winged Barbtail may be most similar to nests of *Pseudocolaptes* tuftedcheeks, which also nest in tree cavities and use tree-fern petiole scales exclusively upon which to lay their eggs (Sclater and Salvin 1879, Skutch 1969, Zyskowski and Prum 1999). The exclusive use of tree-fern petiole scales in nest construction is known only in *Premnornis* and *Pseudocolaptes*, and may be a synapomorphy uniting the two genera (K. Zyskowski pers. comm.). Nest architecture, however, is poorly known in *Pseudocolaptes*. Zyskowski and Prum (1999) classified a single *Pseudocolaptes* nest specimen as a "platform" based on its current shape and because tree-fern petiole scales are too short to be interwoven (a criterion in their "cup" classification scheme). It is important to note, however, that the *Pseudocolaptes* nest could have been cup-shaped prior to being removed from the nest cavity. In fact, the shape of the Rusty-winged Barbtail nest described here changed from a deep cup to a shallow cup as the nestling grew and, because tree-fern petiole scales were not interwoven, the nest did not hold its shape well after being removed from the cavity (authors pers. obs.). Detailed structure and measurement data from a *Pseudocolaptes* tuftedcheek nest inside (i.e., prior to being removed from) its nest cavity could clarify potential nest architecture similarities between *Premnornis* and *Pseudocolaptes*.

Unlike the scansorial habits of *Margarornis* treerunners, Rusty-winged Barbtails searched for arthropod prey by hopping through vine tangles and tree branches, often through dense foliage. Rusty-winged Barbtails acquired prey primarily by gleaning from and probing into dead leaves and moss. Foraging ecology of the Rusty-winged Barbtail, therefore, is similar to that of some foliage-gleaners and *Cranioleuca* spinetails (see Remsen and Parker 1984, Rosenberg 1997), as noted previously by Fjeldså and Krabbe (1990) and Ridgely and Tudor (1994). Quantitative data on the foraging behavior of *Premnoplex* barbtails could yield further insight into ecological variation within the *Margarornis* assemblage.

The unique nesting ecology, and potentially

unique foraging ecology, of the Rusty-winged Barbtail within the *Margarornis* assemblage may imply genetic divergence from the *Margarornis* assemblage or reflect ecological convergence with other furnariid taxa (e.g., *Pseudocolaptes*, various foliage-gleaner genera). Species of the *Margarornis* assemblage, including the Rusty-winged Barbtail, possess numerous myological variations in hindlimb musculature, which appear to be adaptive for tree climbing (Rudge and Raikow 1992a). Based on a series of derived characters, Rudge and Raikow (1992b) hypothesized that the *Margarornis* assemblage represents a monophyletic group and, further, that *Premnornis* and *Premnoplex* are sister taxa. Although resolving the phylogenetic relationships of the Rusty-winged Barbtail is beyond the scope of this paper, we suggest that ecological characteristics of the species are incongruous with its traditional taxonomic position and warrant attention in future phylogenetic analyses.

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DO TWO MURRELETS MAKE A PAIR? BREEDING STATUS AND BEHAVIOR OF MARBLED MURRELET PAIRS CAPTURED AT SEA

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ABSTRACT.—Marbled Murrelets (*Brachyramphus marmoratus*) observed at sea usually are in pairs throughout the year. Although it has been assumed that these pairs are mates, this assumption has not been formally examined. Using data from three study sites during the breeding seasons of 1997–2001, we found that 92% of the birds that were paired at capture were of male-female pairs, and that paired females were more likely (73%) to be producing eggs than were single females (8%). Fourteen of fifteen pairs were tracked to a single nest location per pair. No pair members caught at sea were found breeding at separate nest sites. One pair was caught in two successive seasons, suggesting that at least some pairs are long lasting. Notably, pair members breeding together and radio tracked throughout the summer were detected without their breeding partners for 77% of the time. Thus, while pairs of Marbled Murrelets observed at sea most likely are members of a breeding pair, single murrelets observed at sea should not be assumed to be unpaired or nonbreeders. *Received 9 September 2002, accepted 5 December 2003.*

At-sea surveying is the technique most often employed to census Marbled Murrelets (*Brachyramphus marmoratus*) and to estimate local productivity and population sizes and trends (Sealy and Carter 1984, Piatt and Naslund 1995, Kuletz 1996, Agler et al. 1998, Kuletz and Kendall 1998, Kuletz and Piatt 1999, Speckman et al. 2000). Productivity indices typically are calculated as the proportion of hatch-year to after-hatch-year birds counted at sea (Kuletz and Kendall 1998, Kuletz and Piatt 1999). However, because breeding, subadult, and nonbreeding birds are indistinguishable by plumage (Sealy and Carter 1984), the resulting juvenile:adult ratios are unlikely to accurately represent productivity and census estimates. Murrelet surveyors have reported that Marbled Murrelets at sea most often occur in pairs, during both summer and winter (Sealy 1972, Nelson and Hamer 1995, Strachan et al. 1995), and return to local areas in spring already paired (Sealy 1974). Individuals in pairs exhibit courtship behavior at sea (Nelson and Hamer 1995, Strachan et al. 1995); forage and loaf together (Sealy 1975a, Strachan et al. 1995); call to each other before, during, and after capture (Strachan et al. 1995, Nelson 1997, LMT pers. obs.); and usually are composed of a male and a female (hereafter M-F; Sealy 1972).

These anecdotes suggest that pairs observed at sea are actually mated, breeding pairs (Nelson and Hamer 1995). However, this assumption has not been confirmed (Gaston and Jones 1998). An estimate of the percentage of pairs observed at sea that are indeed mated and breeding together, and an understanding of the status of single birds observed at sea, would improve the accuracy of productivity indices calculated from at-sea surveys, thus allowing more meaningful interpretation of productivity ratios (Evans Mack et al. in press). In addition, information on pair bond maintenance and duration, and the relative use of marine habitat by pair members during the breeding

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TABLE 1. Most Marbled Murrelet pairs are male-female (M-F). One particular M-F pair was captured in both 1998 and 1999 in Desolation Sound.* Data are from British Columbia, Canada.

Variable	Location			
	Mussel Inlet	Desolation Sound	Clayoquot Sound	Total
Years	1997, 1999	1997–2001	2001	1997–2001
Total number of sexed pairs	23	39	2	64
M-F pairs	20 (87%)	37* (95%)	2 (100%)	59 (92%)
M-M pairs	1	1	—	2
F-F Pairs	2	1	—	3
Pairs with egg-producing females	19 (47%)	12 (75%)	—	31 (58%)
M:F sex ratio in dipnet capture sample	—	0.88 (n = 943)	1.19 (n = 79)	0.90 (n = 1022)

season, could be used to determine the optimal time frame to conduct population surveys in the context of breeding chronology, as well as further our understanding of this elusive seabird for which reliable data are difficult to obtain. Our objectives were to (1) test the assumption that M-F pairs were indeed mated, (2) examine the extent and duration of apparent pair bond behavior throughout the breeding season, and (3) examine the amount of time pair members were alone at sea.

METHODS

Study area and captures.—We captured 74 Marbled Murrelet pairs at three locations in British Columbia, Canada: Mussel Inlet (52° 51′ N, 128° 10′ W) during May of 1997 and 1999 (n = 27 birds); Desolation Sound (50° 05′ N, 124° 40′ W) from April to September, 1997–2001 (n = 45); and Clayoquot Sound (49° 12′ N, 126° 06′ W) during May 2001 (n = 2). We used dipnetting (also called "night lighting"; Whitworth et al. 1997, Vanderkist et al. 2000) to capture pairs at night (23:00–05:00 PST) on the open water; we also captured single murrelets that were either (a) obviously paired but whose pair member escaped capture or (b) apparently single at sea, with no partner nearby.

DNA sexing and identifying egg producers.—We determined the sex of 64 of the 74 pairs captured (Table 1). DNA was extracted from red blood cells following the methods in Vanderkist et al. (1999). Egg-producing females were identified by the presence of an egg yolk precursor (vitellogenin) in the plasma, using a diagnostic kit (Zn, Cat. No. 435–14909, Wako Pure Chemical Industries, Ltd.), following the methods of Mitchell and Carlisle (1991) and Vanderkist et al. (2000). We obtained blood samples as described by McFarlane Tranquilla et al. (2003). Plasma samples were available only from birds taken at Desolation Sound (1999–2000) and Mussel Inlet (1997). For birds captured in Desolation Sound, we used exact χ^2 tests to compare the frequency of egg-producing females captured in pairs (n = 64, including females that were paired but whose partner escaped) to those captured alone (singles; n = 12). The mean egg production date plus one standard deviation (16 June) had been previously determined for Desolation Sound (McFarlane Tranquilla et al. 2003), and was used as a cut-off date after which some females would be past egg production and thus were excluded from the analysis. We collected plasma samples in Mussel Inlet during May, within the expected egg-producing period.

Radio tracking.—We used radio telemetry to monitor Marbled Murrelet behavior and daily at-sea attendance and location. Twenty-four Marbled Murrelet pairs received radio transmitters (Model 384 in 1998 and Model 386 in 1999, 2000, and 2001; Advanced Telemetry Systems, Isanti, Minnesota). Transmitters were attached between the scapulars of the birds following the methods of Newman et al. (1999) and Lougheed et al. (2002). The transmitters were deployed during the egg-producing period (20 April to early June), and remained active for a minimum of 80 days. We tracked radio-tagged birds by helicopter every day until 30 August or until the transmitter signal disappeared. Incubating pairs alternate regular 24-h incubation shifts, spend-

ing one day on the nest and the next day at sea, until incubation is complete. Individuals displaying this incubation pattern were classified as breeders; those that did not were classified as nonbreeders (see Bradley and Cooke 2001, Bradley et al. 2002). By monitoring nest attendance patterns, and by extrapolating to the end of incubation and chick-rearing periods (*sensu* Hamer and Nelson 1995), we were able to determine the specific breeding stage (i.e., pre-incubation, incubation, and chick-rearing stages) of radio-tagged pairs. Successful breeders were those radio-tagged individuals for which more than 30 days of incubation shifts were recorded, and were subsequently detected flying inland (presumably to feed chicks) after these incubation shifts ended. Unsuccessful breeders were those whose incubation shifts terminated prematurely and who did not appear to make regular inland flights.

At-sea associations of pair members.—To address the extent and duration of pair member association throughout the breeding season, we compared the behavior of radio-tagged pair members to each other and to other radio-tagged murrelets. We had sufficient data to do this only for Desolation Sound. We used aerial radio telemetry detections for each radio-tagged individual to calculate (1) the amount of overlap of Kernel home ranges between pair members, and (2) direct distances between pair members as detected and geo-referenced from the air. The locations of individuals detected during aerial telemetry flights were geo-referenced to landmarks, and digitized (Bradley et al. 2002) in a Geographic Information System (ArcView ver. 3.2; Environmental Systems Research Inst., Inc. 2000). Because the radio locations spanned the breeding season for most individuals, telemetry locations from each individual were pooled and treated as one record (see Kenward 2001). We used ArcView Animal Movement extension ver. 3.1 (Hooge and Eichenlaub 1997) to calculate the Kernel home range for each radio-tagged Marbled Murrelet having more than 24 telemetry detections, with a nonparametric kernel density estimator, and a fixed kernel method (Seaman and Powell 1996, Seaman et al. 1999, Kenward 2001). We defined core home range (hereafter "home range") as the 30% kernel home range; we chose this conservative cut-off for a more accurate representation of primary habitat use (Samuel et al. 1985, Seaman et al. 1999, Shepherd 2001). We used ArcView to calculate the overlap (weighted percent shared home range area) of home ranges between murrelets.

We used individual home range polygons to calculate the extent of habitat use overlap of 16 individual pair members to (1) their pair partner and (2) to other randomly selected, radio-tagged murrelets that originally had been captured in pairs. To control for potential seasonal differences in reproductive status between randomly selected pair members, our selection of pairs included only those birds captured within <2 days of each other. We used two-sample *t*-tests to compare the overlap of home ranges between 8 pairs and between 22 randomly selected pairs (we used 22 because this was the maximum number of pair combinations we could make).

We were not able to address pair association in each separate breeding stage (pre-incubation, incubation, and chick-rearing) because sample sizes for some pairs were insufficient to calculate separate kernel home ranges at each stage. Instead, we used telemetry detections to assess the distance between pair members, as a measure of spatial association during each breeding stage. From the air, radio-tagged pair members appeared to be either (1) at the same location (together), (2) at different locations in the study area (apart), or (3) alone at sea (alone; i.e., their partners were not in Desolation Sound or the surrounding marine area). For the 8 pairs and 22 randomly selected pairs, we used χ^2 analysis to compare the number of times pair members were together, apart, and alone during the study period.

In six cases, telemetry detections were sufficient to further categorize the spatial association of pair members (i.e., together, apart, alone) according to breeding stage (pre-incubation, incubation, or chick-rearing). For these six cases, we used repeated measures ANOVA to compare the amount of time together, alone, and apart during each breeding stage. Daily detections of radio-tagged murrelets in both pair and randomly selected pair groups were made within a few hours.

TABLE 2. Most Marbled Murrelet pair members, radio-tagged at sea, were tracked to the same nest site location and determined to be breeding together. This was the case in all three study sites. Sexes of some birds were unknown, but most likely were members of M–F pairs since they were tracked to the same nest site. Data are from British Columbia, Canada.

Variable	Location			Total
	Mussel Inlet (1999)	Desolation Sound (1998–2001)	Clayoquot Sound (2001)	
Pair members				
Bred together	6	6	2	14
Neither bred	2	7	0	9
Bred separately	0	0	0	0
Only one bred	0	1	0	1
Total pairs radio-tagged	8 unknown	14 (11 M-F, 3 unknown)	2 M-F	24

RESULTS

Sex ratio in pairs.—Ninety-two percent of sexed pairs (n = 64) were M-F pairs, and 8% were same-sex pairs (Table 1). Given the sex ratio in the capture sample, this percentage of M-F pairs is greater than one would expect based on random association of pair members (for Desolation Sound: χ^2 = 11.25, df = 1, P < 0.007; for Clayoquot Sound: χ^2 = 27.29, df = 1, P < 0.001; Table 1). In Desolation Sound, one M-F pair was captured in both 1998 and 1999, suggesting at least some between-year fidelity.

Egg producers.—Fifty-eight percent of the pairs captured included an egg-producing female (Table 1). We also assessed egg production in paired females (i.e., each paired female captured, whether the other pair member was captured or not) compared to single females. Paired females (73%, n = 64) were more likely to be producing eggs than single females (8%, n = 12; χ^2 = 18.41, df = 1, P < 0.001).

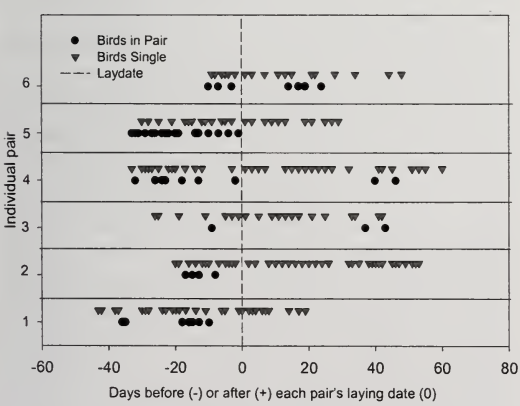

FIG. 1. Marbled Murrelet pair members were detected in pairs (together) prior to laying, and were detected as single birds (either apart or alone) for most of the breeding season. Some pair members were together after the incubation stage. Data are from British Columbia, Canada, 1997–2001.

Radio-tagged pairs.—We detected incubation behavior for 63% (15/24) of the radio-tagged pairs (Table 2). Of the 15 pairs showing incubation behavior, 14 were radio tracked to a single nest location per pair. No radio-tagged pair members were found breeding at separate nest sites (Table 2). In one pair, the female appeared to be incubating a month after capture while the male of this pair behaved as a nonbreeder throughout the season.

At-sea associations of pair members.—The home range size of pairs (n = 8) and randomly selected pairs (n = 22) was not significantly different (two-sample t = 0.54, df = 33, P = 0.59). However, the percent shared home range area between pair members (53.3% ± 7.1 SE) was significantly greater than that shared by randomly selected pair members (30.1% ± 5.2 SE; two-sample t = 2.64, df = 22, P = 0. 015). Members of pairs were detected together 40.0% ± 6.7 SE of the time. This was significantly greater than for randomly selected pairs detected together (11.0% ± 1.2 SE of the time; two-sample t = 4.27, df = 7, P = 0.004).

For six pairs with sufficient data to assess associations during each breeding stage (Fig. 1, Table 3), pair members were detected together more frequently during the pre-incubation stage (34%) than during the incubation

TABLE 3. The members of six pairs of radio-tagged Marbled Murrlets most often were detected alone (at sea) or apart (in different locations in the same study area), and thus appeared as single birds. Values within the table are percentages of detections; values in parentheses are mean number of detections per pair. Data are from Desolation Sound, British Columbia, Canada, 1998–2001.

	Breeding stage			
Attribute	Pre-incubation ($\bar{x}$ = 35)	Incubation ($\bar{x}$ = 21)	Chick-rearing ($\bar{x}$ = 12)	Total ($\bar{x}$ = 67)
Alone	26	93	70	53
Apart	39	2	10	24
Together	34	5	20	23

or chick-rearing stages (repeated measures ANOVA, Wilk's Lambda = 0.38, $F_{2,6} = 4.9$, $P < 0.055$; Table 3). During the pre-incubation stage, pair members would have appeared to the at-sea observer as single (i.e., either alone or apart) for 65% of the time (Table 3). Pair members were alone most often during the incubation stage (93%). One pair appeared to fail during incubation and re-associated after this event (Fig. 1, pair 6). Overall, these six radio-tagged pair members at sea were single (either apart or alone) 77% of the time, and together 23% of the time (Table 3; test for two proportions, $Z = 9.07$, $P < 0.001$). Radio-tagged pair members that were successful breeders ($n = 6$) were detected together for a significantly longer duration (55.0 days ± 29.4 SD) than those that were unsuccessful breeders ($n = 5$; 19.4 days ± 18.5 SD); ANOVA, $F_{1,9} = 5.5$, $P = 0.044$).

DISCUSSION

Our data suggest that a large majority of Marbled Murrelets caught or observed together as pairs early in the breeding season are mated pairs. Most pairs at sea were of opposite sex, nested together, associated more at sea, and shared a greater proportion of home range area with each other than with randomly selected pair members. Nevertheless, we found that pair members spent more than half of their time alone or apart from each other at sea. Not only were pair members detected at sea as singles during incubation (as in Sealy and Carter 1984, Evans Mack et al. in press), but they also were single for more than half of all telemetry detections throughout the breeding season.

Our study confirms the findings of Sealy (1975b), who also found most Marbled Murrelet pairs to be male-female pairs. The few same-sex pairs we found may have been together while their mates were incubating (Evans Mack et al. in press). Although there is little evidence that Marbled Murrelets forage at night (Jodice and Collopy 1999, but see Strachan et al. 1995), Marbled Murrelets often forage together in pairs during the day (Hunt 1995, Strachan et al. 1995), which likely increases foraging efficiency (Sealy 1972). Thus, the occurrence of same-sex pairs at night may be due to associative foraging. Alternatively, same-sex pairs may have been captured together coincidentally.

The strongest support for the assumption that pair members are mated came from the confirmation that all pairs that bred did so together, each pair at a single nest site. Only one pair appeared to divorce; in this case, either the male did not participate in incubation, was replaced as a mate, or may have been captured coincidentally near the female. Additional support that pair members are breeding together comes from our finding that during the laying period, 73% of pairs contained an egg-producing female.

Although murrelets captured in pairs were breeding together, radio-tagged pair members most often were away from their partners at sea. Without concurrent at-sea surveys, we cannot confirm that pair members found alone or apart by aerial radio telemetry were actually separate from other untagged murrelets at sea (as in Evans Mack et al. in press). Despite the amount of time spent alone, the marine home ranges of pair members overlapped more with their mates than with other radio-tagged murrelets. Because the 30% kernel home range is considered an accurate description of the area used most frequently by an animal (Samuel et al. 1985), we are confident that the home range overlap is a real phenomenon. This suggests that although marine "hotspots" are used by many murrelets, paired murrelets maintain a type of home range at sea, perhaps used more for foraging or loafing with their partners than with other murrelets. The significance of fidelity to and

defense of marine home ranges by murrelets is currently unexplored.

Murrelet pair members are assumed to maintain pair bonds throughout the year (Sealy 1974, Nelson and Hamer 1995). However, prior to this study, there have been no confirmed observations of breeding pairs maintaining a pair bond. We found one-third of murrelet pairs together during the pre-incubation stage and after chick rearing (Table 3), and one pair together in consecutive seasons. We also detected three pairs together during incubation at least once; at-sea associations of pair members during incubation may correspond with skipped incubation shifts (Bradley et al. in press). Remaining associated throughout the breeding season probably increases foraging efficiency (Sealy 1972) and promotes pair fidelity for future years (Nelson 1979). However, as in other species, pair bonds may break down following a failed reproductive event. Consistent with this idea, members of successful breeding pairs were detected together for longer than unsuccessful pairs.

As Kuletz and Kendall (1998) suggested, numbers of breeding-plumaged adults present during early incubation would more accurately reflect the local breeding population than those present during late summer. Further, we suggest that the number of pairs observed during the pre-incubation stage can provide an estimate of breeding attempts when calculating productivity, but we caution that failed breeders also may appear in pairs.

Finally, surveyors should be aware that although pairs at sea are likely mated, pair members at sea spent only 20–40% of their time together throughout the breeding season, including during the pre-incubation stage when they are expected to be together the most. Thus, the presence of single murrelets at sea is probably not suitable to infer incubation periods, numbers of nonbreeders, or numbers of failed breeders. However, as Evans Mack et al. (in press) suggest, the proportion of single murrelets during the incubation period may help assess the proportion of nesting murrelets. We support this suggestion because our pairs were separate 95% of the time during incubation (Table 3). At the same time, we caution at-sea surveyors to use additional methods (Hamer and Nelson 1995, Lougheed et al. 2002, McFarlane Tranquilla et al. 2003) to determine breeding phenology at a local scale in order to make more accurate estimates of breeding pair numbers. Because pairs spent most of their time alone throughout the season, single murrelets in the study area at any time can not be assumed to be unpaired or failed breeders.

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HABITAT USE OF SYMPATRICALLY NESTING FISH CROWS AND AMERICAN CROWS

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ABSTRACT.—We examined habitat use of sympatric Fish Crows (*Corvus ossifragus*) and American Crows (*C. brachyrhynchos*) nesting in the vicinity of waterbird breeding locations at the Rockaway Peninsula, New York City. Fish Crows nested significantly more often at natural habitats, including coastal dunes and salt marsh islands; American Crows nested significantly more often at residential and recreational areas. In regard to potential foraging areas, Fish Crows nested closer to waterbird colonies and to the water's edge while American Crows nested closer to a garbage source and to lawns. Fish Crows nested significantly more often in deciduous trees that were native, while American Crows nested significantly more often in evergreen trees that more frequently were exotic, especially Japanese black pine (*Pinus thunbergii*). Finally, we consider the potential predatory impact of sympatric crow species on waterbirds in light of their habitat use. *Received 4 February 2003, accepted 25 September 2003.*

Fish Crows (*Corvus ossifragus*) and American Crows (*C. brachyrhynchos*) are common corvids in North America, yet limited information is available about their basic biology and interactions in sympatry (McGowan 2001, Verbeek and Caffrey 2002). Fish Crows occur along the Atlantic and Gulf coasts as well as connecting rivers where they are sympatric with American Crows, which are distributed across North America. Both species build stick nests at the tops of trees and have an omnivorous diet that includes fruits, grains, insects, earthworms, human garbage, bird eggs, and chicks.

Fish Crow and American Crow populations are increasing across their ranges, including metropolitan areas where they appear to adapt to city conditions (Gorenzel and Salmon 1992, McGowan 2001, Verbeek and Caffrey 2002). This is a conservation concern for urban bird species already stressed by habitat loss and human disturbance, since crows are egg and chick predators. Avian taxa susceptible to crow predation include waterbirds, such as terns, skimmers, herons, and especially the endangered or threatened Piping Plover (*Charadrius melodus*; U.S. Fish and Wildlife Service 1985; Lauro and Tanacredi 2002).

Their geographic distributions suggest that Fish Crows are coastal specialists while American Crows are generalists across their range. Thus, we examined the hypothesis that within an area of sympatry at the Rockaway Peninsula, New York City, Fish Crows would select natural, coastal habitats where waterbirds concentrate while American Crows would utilize all available habitats including natural, coastal areas and sites of human habitation.

METHODS

Study area.—We conducted the study during 1998 along the Rockaway Peninsula at the western tip of Long Island, New York (40° 35′ N, 75° 53′ W), at Gateway National Recreation Area, a unit of the National Parks System, and in the surrounding residential community. Locations studied included Breezy Point to Riis Park, Floyd Bennett Field, and several salt marsh islands in Jamaica Bay. More natural environments occur within the park while humanized sites occur mainly at the Breezy Point Cooperative, a residential area, and at recreational and administrative sites within the park.

Breezy Point is at the tip of the Rockaway Peninsula, west of the Cooperative, and is approximately 16 km southeast of Manhattan, extending into New York Harbor. It contains barrier beach habitat uninhabited by humans, with shoreline dunes dominated by American beachgrass (*Ammophila breviligulata*). The

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center area contains woody shrubs, primarily bayberry (*Myrica pensylvanica*), with scattered small trees, including black cherry (*Prunus serotina*). The dune area is a nesting location for Piping Plovers, Herring Gulls (*Larus argentatus*), Great Black-backed Gulls (*L. marinus*), Roseate Terns (*Sterna dougallii*), Common Terns (*S. hirundo*), and Least Terns (*S. antillarum*; Gilmore et al. 1998).

We studied three uninhabited salt marsh islands that had trees suitable for crow nesting, Canarsie Pol, Ruffle Bar, and Little Egg. These islands have dredge spoil deposits at middle to late successional stages, dominated by black cherry, black locust (*Robinia pseudoacacia*) and eastern cottonwood (*Populus deltoides*). Each of the islands has a Herring Gull and Great Black-backed Gull nesting colony. Canarsie Pol has a mixed species heronry with Great Egrets (*Ardea alba*), Snowy Egrets (*Egretta thula*), Little Blue Herons (*E. caerulea*), and Glossy Ibises (*Plegadis falcinellus*).

Habitat use.—We examined all accessible locations in the study area for nesting crows weekly during 1998, beginning 15 March and continuing through the end of nesting in August. We collected habitat use data for first nests only. We examined habitat use at three different scales: general habitats, territories, and nest sites, as it is believed that birds select habitats in this order (Burger 1985, Klopfer and Ganzhorn 1985, Sherry and Holmes 1985).

We designated the general habitat type for each nest as either peninsula or salt marsh island. The category of peninsula included the areas from the tip of Breezy Point to Riis Park and Floyd Bennett Field. We compared the peninsula (1,022 ha) and salt marsh islands (151 ha) with respect to nesting density (pairs/ha) of the species present. All environments were included for calculations since crow territories occurred across all spaces.

To examine territory and nest site use, we measured physical and vegetative characteristics around the nest tree and of the nest tree itself. Where applicable, we measured the same physical and vegetative characteristics at a random site within a 100-m radius of each nest. We determined the location of the random point by selecting a direction (north, south, east, or west) and then a distance (between 1 and 100 m) using a random numbers table.

We measured territory characteristics, including distance from nests to potential feeding areas at the waters edge, a waterbird colony, a lawn, and a garbage container. To characterize nest location relative to human habitation, we measured distance to nearest building. Other territory attributes we measured included distance to the nearest tree, to the edge of a patch of woods, and to the nearest conspecific neighbor, as well as the number of trees, scrub height, and percentage of scrub within a 10-m circle of the nest.

To examine nest site use we identified nest tree species and determined whether it was native or exotic. We also measured nest tree height and nest height using a clinometer. We recorded the number of limbs upon which the nest was placed and the diameter of the tree (dbh). Finally, we estimated visibility from nest sites as the degrees of a circle visible to a bird sitting on a nest.

RESULTS

General habitat and territory use.—Fish Crows nested more frequently at natural coastal environments while American Crows nested more frequently at residential and recreational locations. We located 19 Fish Crow nests: 2 at Breezy Point, and 17 on salt marsh islands. We located 23 American Crow nests on the Peninsula at residential and recreation locations; no nests were located at Breezy Point or on salt marsh islands. Compared to American Crow nests, Fish Crow nests were significantly closer to water and to a waterbird colony, but significantly farther from buildings, garbage sources, and lawns (Table 1).

Fish Crow nesting density was higher on salt marsh islands (0.113 pairs/ha) than on the peninsula (0.002 pairs/ha), and was higher on salt marsh islands than American Crow densities on the peninsula (0.023 pairs/ha). Nearest conspecific neighbor distances for nesting Fish Crows were significantly less than those for American Crows (Table 1).

Nest site use.—Fish Crows nested more frequently in deciduous (94%) than in evergreen (6%) trees. However, the habitats where Fish Crows nested had mainly deciduous trees (100% of the randomly selected trees) and few evergreens, providing little opportunity for

TABLE 1. Characteristics of Fish Crow (n = 17) and American Crow (n = 23) nest sites and random sites. Fish Crows selected nest sites in more natural habitats, especially near waterbird colonies, while American Crows selected nest sites at residential and recreational locations. Data are from western Long Island, New York, 1998. Test statistics and probabilities are from Wilcoxon two-sample tests.

	Fish Crow					
	Nest site		Random site		Site comparisons	
	Mean	SE	Mean	SE	Z	P
Distance (m) of nest to						
Conspecific neighbor	139	23	—	—	—	—
Water	166	32	176	35	−0.19	0.8497
Waterbird colony	10	5	7	3	−0.14	0.8886
Building	1,479	110	1,495	103	0.04	0.9725
Garbage container	1,479	110	1,496	102	0.05	0.9725
Lawn	1,524	87	1,532	86	0.00	1.000
Patch edge	6	2	5	2	−0.42	0.6742
10-m circle around nest						
Number of trees	18	6	10	4	1.12	0.2619
% scrub	63	7	56	7	0.88	0.3785
Scrub height (cm)	72	18	50	11	0.22	0.8228
Nest tree						
Nearest tree (m)	14.4	5.5	24.0	8.6	−1.33	0.1846
DBH (cm)	81.8	31.4	31.3	7.1	1.66	0.0975
Tree height (m)	9.4	1.5	5.7	0.5	1.67	0.0946
Nest height (m)	7.1	1.1	—	—	—	—
Visibility (degrees)	195	29	—	—	—	—
Number of tree limbs supporting nest	3	0.3	—	—	—	—

choice. This habitat also provided a nearly even mix of native (48%) and exotic trees (52%), but Fish Crows nested significantly more frequently in native (82%) than in exotic (18%) trees (χ^2 = 4.64, df = 1, P = 0.031).

In contrast, American Crows nested more frequently in evergreen (65%) than in deciduous (35%) trees, which differed significantly from their availability at random sites (30% versus 70%, respectively; χ^2 = 5.58, df = 1, P = 0.018). American Crows also nested more frequently in exotic (74%) than in native (26%) trees, but this difference was similar to the availability of exotic and native trees at random sites (57% and 43%, respectively; χ^2 = 1.53, df = 1, $P > 0.23$). Fourteen of the fifteen evergreen nest trees were the exotic Japanese black pine (*Pinus thunbergii*); the one native evergreen nest tree was a Red Cedar (*Juniperus virginiana*).

A trend for both crow species was to select nest trees that were larger than those available (Table 1). Both species selected trees that were significantly taller than random trees, and the mean dbh values were greater than those of random trees, although they were not significantly different. The evergreen trees were taller than the deciduous trees in our study area, so American Crows nested in taller trees than did Fish Crows. Furthermore, American Crows selected nesting areas where tree density (measured by number of trees/10-m circle, and distance to nearest tree) was significantly greater than in surrounding random sites (Table 1). No significant differences were found for Fish Crows for similar comparisons, although mean values showed a similar trend to that of American Crows (Table 1).

Both species placed nests about 2 m from the tops of trees in a crotch that contained a mean of 3 limbs, with a mean visibility ≥195° (Table 1). The areas underneath deciduous trees where Fish Crows nested had more scrub compared to the areas underneath evergreens where American Crows nested as indicated by significant differences in species comparisons for nest and random locations (Table 1).

DISCUSSION

We found support for the hypothesis that Fish Crows are more closely associated with

TABLE 1. EXTENDED

American Crow						Species comparisons			
Nest site		Random site		Site comparisons		Nest sites		Random sites	
Mean	SE	Mean	SE	*Z*	*P*	*Z*	*P*	*Z*	*P*
625	63	—	—	—	—	−4.90	0.0001	—	—
361	54	317	45	0.49	0.6208	−2.77	0.0057	−2.22	0.0267
3,242	205	3,248	205	−0.08	0.9387	−5.39	0.0001	−5.26	0.0001
186	64	181	70	0.05	0.9562	5.12	0.0001	5.06	0.0001
111	62	85	26	−1.29	0.1985	5.15	0.0001	5.34	0.0001
75	22	85	26	0.62	0.5346	5.34	0.0001	5.37	0.0001
6	2	5	2	0.94	0.3469	0.44	0.6596	1.07	0.2868
10	2	6	1	1.80	0.0722	0.14	0.8910	−0.91	0.3629
34	8	29	7	0.45	0.6501	2.61	0.0091	2.54	0.0111
25	8	25	7	0.07	0.9471	2.41	0.0159	2.62	0.0089
2.3	0.5	3.6	0.5	−1.90	0.0574	0.81	0.4196	1.89	0.0591
65	9.6	55.4	7.9	0.46	0.6445	−0.90	0.3683	−2.27	0.0231
11.6	0.6	8.3	0.7	3.19	0.0014	−2.30	0.0214	−2.70	0.0070
9.9	0.7	—	—	—	—	−2.69	0.0076	—	—
251	22.0	—	—	—	—	−1.78	0.0744	—	—
2.9	0.2	—	—	—	—	−0.19	0.8480	—	—

coastal environments where waterbirds concentrate than are American Crows. Fish Crows nested more frequently in natural habitats within the National Park, including the dune area at Breezy Point and salt marsh islands in Jamaica Bay. However, results suggested that at this study site American Crows were not generalists across all habitats as they showed a greater association with areas of human habitation. American Crows nested most frequently at recreational areas within the National Park and at residential and commercial areas along the Rockaway Peninsula.

One possible explanation for the differences in general habitats between the two species at this area may be related to preferred prey within nesting territories. Fish Crows selected habitats that provided ready access to waterbird eggs and chicks, as evidenced by the significantly shorter distances to a waterbird colony; all Fish Crow nests were within a waterbird colony. At the Breezy Point tip, Fish Crows nested at the center of a gull colony where they systematically hunted their surrounding territory for food, including the shore edge where Piping Plovers nested. Moreover, an artificial nest study at this site revealed that crows were a more serious predator of waterbird eggs than other potential predators, including gulls (Lauro and Tanacredi 2002). Although crow species distinctions were not made in that study, it is likely that Fish Crows were the main crow predator since they were the only crow species to defend territories at the tip. On the islands of Canarsie Pol and Ruffle Bar (Piping Plovers did not nest here) we observed collections of predated heron and gull eggs under Fish Crow nests. Fish Crows are well known predators of waterbird eggs at coastal areas and other studies have documented that they create middens of predated eggs (Kalmbach 1939, Bent 1946, Burger and Hahn 1977, Shields and Parnell 1986, Massey and Fancher 1989, Post 1990, Lauro and Tanacredi 2002).

All American Crow territories were either completely within or on the edge of residential and recreational areas, and no nests were found at gull colonies or heron colonies during this study. Throughout the study area we

regularly observed American Crows foraging on garbage and on lawn invertebrates. American Crows also are well known predators of bird eggs and chicks, and we observed them foraging on beaches that bordered residential and park regions where waterbirds nested. During this study American Crows preyed upon Piping Plover eggs and chicks (Gilmore et al. 1998). Thus, this study and others suggest that although both species of crows are predators of waterbird eggs and chicks, Fish Crows may be specialists for this type of prey.

Another factor contributing to species differences in general habitat may be related to preferred nest tree type. American Crows selected evergreen trees while Fish Crows nested mainly in deciduous trees. Other studies suggest that American Crows prefer coniferous trees (Bent 1946, Chamberlain-Auger et al. 1990). Therefore, American Crows may have avoided natural habitats because they had fewer suitable trees for nesting. Evergreens provide year round protection from the elements, and cover from predators, compared to deciduous trees that have minimal protection prior to leafing out. This may be important to American Crows which maintain year round territories (Stouffer and Caccamise 1991, Caccamise et al. 1997) and perhaps facilitates earlier nesting.

Our results suggest that the practice of planting exotic evergreens, such as Japanese black pine, along barrier islands may be a conservation concern since it will likely encourage American Crow nesting, potentially increasing waterbird predation. Another study conducted in Massachusetts in natural and suburban environments found 100% of nests were in evergreen trees, but 96% of these were in native species (Chamberlain-Auger et al. 1990). Thus, the native versus exotic status of evergreens may not be important to American Crow nesting. However, to avoid the potential risk of predation to waterbird eggs and chicks by American Crows, it might be advisable not to plant evergreens in dense groves.

A greater number of differences were found for species comparisons of habitat characteristics at nest sites and at random sites than were found for nest versus random comparisons within each species. This was a reflection of the different types of general habitats that the two species selected and of the importance of tree type compared to other characteristics measured.

In conclusion, results suggested that at this study area Fish Crows are coastal specialists while American Crows are human habitation specialists, possibly minimizing interspecific interaction and facilitating their coexistence. However, this may be a site specific phenomenon, so it would be valuable to study other locations to determine if the same pattern holds true. Given the territorial behavior of American Crows and Fish Crows (Caccamise et al. 1997, McGowen 2001, Verbeek and Caffrey 2002) and given that Fish Crows nested more frequently in areas where waterbirds nested, Fish Crows likely would be the more serious predator. However, at this location and perhaps at others, the greatest threat to waterbird eggs and chicks may occur at edge locations where natural and humanized sites meet, since both crow species may maintain territories here.

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GRASSLAND SONGBIRD NEST SITE SELECTION PATTERNS IN NORTHCENTRAL MONTANA

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ABSTRACT.—We explored nest site habitat selection patterns for six grassland passerine species in northcentral Montana: Sprague's Pipit (*Anthus spragueii*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Baird's Sparrow (*A. bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). We quantified habitat characteristics at sites chosen for nesting and compared them to randomly selected sites, both spatially and temporally. Using discriminant analysis, two species groups were discernable based on a combination of habitat characteristics, which were distinct from random sites. Nest sites had greater foliage height and density than random sites. This pattern generally was shown most strongly by Western Meadowlarks, Baird's, and Savannah sparrows. Three bird species selected nest patches (5-m radius plots centered on nests) having little or no clubmoss (*Selaginella densa*) cover, which was one of the most powerful discriminating variables in this analysis. The conservation implications of increasing clubmoss cover in relationship to nest site selection in northern Great Plains grasslands are discussed. *Received 20 May 2003, accepted 15 August 2003.*

Grassland bird abundance of the Great Plains has declined at a greater rate than for any other avifaunal group in North America (Knopf 1994, Sauer et al. 2001). This has been attributed to habitat conversion (e.g., cultivation and woody vegetation encroachment; Houston and Schmutz 1999), removal of native grazers and fire (Knopf and Samson 1997), and increased predation and brood parasitism (Basore et al. 1986, Davis and Sealy 2000). Avian conservation requires information on nest site habitat selection, which is virtually nonexistent for many grassland songbird species that breed in the northern prairie. Consequently, we quantified spatial and between-season nest site selection patterns for six grassland passerine species that co-occur in northcentral Montana: Sprague's Pipit (*Anthus spragueii*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Baird's Sparrow (*A. bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Discerning habitat differences in nest site selection may enable us to better understand how subtle changes in habitat characteristics of northern grasslands could impact the community composition and distribution of bird species that breed there.

METHODS

Study area.—We conducted the study at Bowdoin National Wildlife Refuge in Phillips County, northcentral Montana (48° 24′ N, 107° 39′ W; elevation about 750 m). The study area consisted of flat to gently rolling native mixed grass prairie. The climate is continental and semiarid, exhibiting strong winds and high evaporation rates. Long term annual and seasonal (May to July) precipitation totals are 33.7 and 18.2 cm, respectively. Mean annual and seasonal precipitation totals were 30.6 and 15.5 cm, respectively, during the study. Herbaceous dominants included western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), clubmoss (*Selaginella densa*), and fringed sagewort (*Artemisia frigida*). Shrubs (*Sarcobatus vermiculatus*, *Artemisia cana*, *Ceratoides lanata*) were sparse, and trees absent, except sporadically outside the border of the study area. The study area has not been grazed consistently for >25 years. A small portion of the study area burned in 1994; otherwise, no burning events have occurred since refuge documentation began in 1936.

Nest searching.—We collected data during the summers of 1998–2001 on four study sites (26–59 ha; 180 ha total) situated 1.6–3.8 km apart around Lake Bowdoin. We searched

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these sites for nests 3–5 times per week from mid-May through mid-August in an attempt to locate all active nests. Search techniques included behavioral observations (Martin and Geupel 1993), foot flushes, and rope drags using a single, weighted 30-m length of rope with cans attached at 1-m intervals (S. Davis pers. comm.). Ropes were pulled systematically across each study site while observers carefully watched for females flushed off nests. Once located, nests were marked for relocation and monitored every 2–4 days.

Nest site measurements.—Following nesting termination, we took measurements directly at the nest (nest site), within a 5-m radius plot centered around each nest (nest patch), and at random 5-m radius plots (n = 250). We crossed each plot with two 10-m transects placed perpendicularly across the center of the plot, and took measurements at the nest (or center point of random plots), and at 1-, 3-, and 5-m intervals outward in each cardinal direction. Measurements included plant height, litter depth, visual obstruction, and vertical vegetation density. We estimated visual obstruction by measuring the height at which a 15-mm diameter pole was completely obscured by vegetation when viewed at a height of 1 m and a distance of 4 m (Robel et al. 1970). We quantified vertical vegetation density by summing the number of vegetation contacts on a pole held vertically at each sample point (Wiens 1969). We visually estimated the percent cover of the following physiognomic categories for each patch: bare ground, cactus (*Opuntia polyacantha*), clubmoss, forb, grass, litter, rock and gravel, sedge (*Carex* spp.), and shrub. Additional measurements at the nest included topographic slope and identification of plant species at the placement of the nest (sedges were identified to genus).

Data analysis.—We conducted statistical analyses using SPSS ver. 10.0.5 (SPSS, Inc. 1999), and we performed Box-Cox transformations using Minitab ver. 12.1 (Minitab, Inc. 1998). In addition to examining nest site differences among the six bird species, we also treated random plots as a separate, independent statistical group, allowing us to compare habitat use to what generally was available within the study area. Habitat variables first were summarized at the univariate level, mainly to report individual effect sizes. This included a check for redundancy by estimating total correlation coefficients for all combinations of variables. Relative frequency of the dominant plant species at the nest was estimated for each bird species and differences tested for statistical significance (χ^2 test). We also performed a 1-way ANOVA on continuous variables to test for differences among bird species. We conducted *post hoc* comparisons using Dunnett's pairwise multiple comparison t-test, which compared each species to the means generated from random plots. Strength of association was summarized using the proportional reduction in error measure (adjusted R^2), which was interpreted as the amount of variance in each habitat variable explained by bird species. We used Goodman and Kruskal's tau (τ) as a proportional reduction in error measure for plant dominants (Agresti and Finlay 1986). We transformed data when assumptions of within-group normality and equal variances were grossly violated (arcsine for percentages <30 or >0, Box-Cox procedures elsewhere).

We then used discriminant function analysis (DFA) to evaluate habitat differences among bird species at the multivariate level. Only statistically significant variables at the univariate level were included in the DFA. We used structure coefficients to interpret the individual functions. These are simple linear correlations between the habitat variables and discriminant functions; consequently, each function can be "named" according to the variables with the highest correlations. The use of structure coefficients as a basis for interpretation is advantageous over weighted coefficients since they are less affected by multicollinearity (Klecka 1980). The overall contribution of individual variables weighted across all significant functions was quantified using the potency index, which is a relative measure of the overall discriminating power of each habitat variable (Hair et al. 1992). Finally, we performed a classification procedure to provide a measure of strength of group separation, when considered relative to the expected classification based on chance alone. We employed jackknife procedures when testing the accuracy of the classification matrix, whereby each data case was classified using functions derived using all other data cases (SPSS, Inc. 1999).

TABLE 1. Nest sites of six songbird species and randomly selected plots in northcentral Montana, 1998–2001. All habitat variables except sedge and shrub cover differed among bird species, although the strength of association (R^2) generally was weak. Bird species was the strongest predictor of clubmoss cover, visual obstruction at the nest, and mean litter depth. For each habitat variable, the values for each bird species are compared to those of random plots (Dunnett's t test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

	Sprague's Pipit		Savannah Sparrow		Grasshopper Sparrow	
Habitat variable	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Bare ground cover (%)	0.7	1.5	0.6	1.4*	0.4	0.8*
Cactus cover (%)	0.8	1.2**	1.0	1.2**	1.6	2.5
Clubmoss cover (%)	22.0	15.4	4.6	8.1***	20.1	11.9
Forb cover (%)	14.5	7.7	13.7	10.1	12.2	6.8
Grass cover (%)	50.2	12.9	65.5	16.4***	56.2	16.5
Litter cover (%)	10.9	9.8***	13.4	9.4***	6.1	3.9
Rock cover (%)	0.5	1.1	0.1	0.4***	0.8	2.6
Sedge cover (%)	1.4	3.8	0.6	2.1	1.9	4.8
Shrub cover (%)	0.5	1.6	0.5	1.8	0.8	3.0
Litter depth (cm)	11.2	8.8*	21.2	13.5***	9.4	7.6
Visual obstruction-nest (dm)	1.4	0.4***	1.7	0.5***	1.3	0.4***
Visual obstruction-plot (dm)	0.9	0.4	1.3	0.5***	0.9	0.4
Slope (°)	0.6	0.7	0.4	1.2	1.4	2.2
Plant height-nest (cm)	31.7	15.2**	34.3	12.1***	32.5	15.1***
Plant height-plot (cm)	25.9	7.2	31.6	7.4***	23.6	8.3
Vertical density-nest	4.3	3.9	5.4	3.7***	5.5	4.4**
Vertical density-plot	4.4	1.7	6.0	2.5***	4.4	1.9

We explored temporal variation in the dominant nest site habitat characteristics for Savannah Sparrows and Chestnut-collared Longspurs, relative to changes in habitat conditions encountered on the study area. We summarized degree of annual variation within bird species and interactions between bird species and random plots using the proportional reduction in error measure (adjusted R^2).

We treated the nest site (and patch) as independent sample units. Given the spatial proximity of the four study sites, statistical inference (at a significance level of $P < 0.05$) is restricted to the four study sites collectively, during the time period studied.

RESULTS

We located 544 nests during 1998–2001. Chestnut-collared Longspurs were the most abundant (48%, $n = 262$ nests), followed by Savannah Sparrows (21%, $n = 113$), Western Meadowlarks (9%, $n = 49$), Sprague's Pipits (8%, $n = 45$), Grasshopper Sparrows (8%, $n = 42$), and Baird's Sparrows (6%, $n = 33$). We took habitat measurements at an additional 250 randomly selected plots evenly distributed across years.

Univariate analyses.—The total correlation matrix showed two sets of variables with correlations higher than $|0.7|$: clubmoss cover was negatively correlated with grass cover ($r = -0.716$), and visual obstruction at the nest was strongly correlated with visual obstruction within the nest patch ($r = 0.800$).

Metric habitat variables differed among bird species at the univariate level, except sedge and shrub cover ($P > 0.05$; Table 1). Strength of association for most variables was weak ($R^2 < 0.10$), particularly among the cover variables. However, clubmoss cover showed the greatest separation ($R^2 = 0.371$), followed by visual obstruction at the nest ($R^2 = 0.310$) and mean litter depth within the nest patch ($R^2 = 0.246$).

Over 99% of all nests were placed adjacent to or within 24 identified plant species. About 70% used needle-and-thread, western wheatgrass, or blue grama as the nesting substrate, which also were the dominant plant species (72%) on the study area. Proportional use of these plant dominants varied significantly among bird species, although the strength of association for these variables was weak (Table 2).

Multivariate analysis.—Six discriminant functions were derived, but only the first three

TABLE 1. EXTENDED

Baird's Sparrow		Chestnut-collared Longspur		Western Meadowlark		Random		
$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	R^2
0.2	0.3**	1.0	11.4	1.4	3.3	1.5	3.8	0.021
0.9	1.2	1.3	1.7*	1.4	2.1	1.8	2.4	0.022
4.8	6.5***	25.1	14.0***	5.1	7.3***	21.3	15.2	0.371
11.9	9.3	15.6	7.5*	9.7	6.4***	13.6	6.9	0.042
70.8	13.6***	48.6	1.7	70.0	14.5***	51.9	16.9	0.192
11.2	5.6***	6.0	2.7	11.0	8.4***	7.5	7.6	0.135
0.0	0.0**	0.6	2.0	0.6	1.9	0.7	2.1	0.039
0.8	2.8	1.0	2.9	0.6	2.4	0.7	1.8	0.007
0.4	0.8	0.9	5.2	0.4	1.3	0.9	2.9	0.000
21.3	12.2***	6.5	0.1	17.6	10.5***	8.9	10.5	0.246
1.8	0.5***	1.1	2.5***	1.8	0.5***	0.9	0.6	0.305
1.4	0.5***	0.7	0.3***	1.2	0.6***	0.9	0.5	0.201
0.5	0.9	0.9	0.3	1.0	2.1	0.8	1.2	0.014
34.9	8.0***	30.2	5.9***	39.1	14.5***	24.1	15.3	0.096
33.6	7.5***	24.9	7.4	31.8	10.7***	24.2	10.2	0.121
5.1	4.5	4.1	11.7	7.5	5.5***	3.5	3.1	0.058
6.3	2.5***	3.7	1.5	5.8	1.9***	4.0	2.2	0.174

were statistically significant (Wilk's lambda, $P < 0.05$; Table 3). The first two functions accounted for over 88% of the total discriminating power of DFA. The dominant habitat variables for the first discriminant function included clubmoss cover ($r = -0.697$), mean litter depth ($r = 0.629$), visual obstruction at the nest ($r = 0.746$) and nest patch ($r = 0.540$), and grass cover ($r = 0.538$). The second function was most correlated with the presence of western wheatgrass at the nest ($r = 0.382$). Overall, vegetation obstruction at the nest, clubmoss cover, and mean litter depth had the highest potency index.

The strength of the discriminant functions in separating groups is indexed by canonical correlation coefficients. The first function was the most powerful ($R = 0.654$), followed by the second function ($R = 0.555$), suggesting that the second function is nearly as important as the first function in its substantive utility. Overall, we correctly classified 54.4% of the data cases, which is greater than what would be expected by chance alone (14.3%). However, successful classifications were largely restricted to random plots and Chestnut-collared Longspurs, both of which showed a large degree of separation relative to the other bird

TABLE 2. Relative frequencies among dominant nesting substrates at nest sites of six songbird species and at randomly selected plots in northcentral Montana, 1998–2001. Among 24 plant species, blue grama, needle-and-thread, and western wheatgrass were the dominant vegetation on the study area and most frequently used as nesting substrates. Selection patterns varied among bird species, although collectively, strength of association (τ) between plant and bird species was weak. For each plant species, values for each bird species are compared to those of random plots (Bonferroni procedure: *, $P < 0.01$; **, $P < 0.001$).

Plant species	Sprague's Pipit	Savannah Sparrow	Grasshopper Sparrow	Baird's Sparrow	Chestnut-collared Longspur	Western Meadowlark	Random	τ
Blue grama	17.8	4.5	31.0*	0.0	21.1*	2.1	12.0	0.010
Needle-and-thread	40.0	17.3	35.7	15.2	39.1	16.7	30.8	0.008
Western wheatgrass	24.4	45.5*	4.8*	57.6*	8.8**	37.5	29.2	0.030
n	45	110	42	33	261	48	250	

TABLE 3. Discriminant function analysis of nest site habitat characteristics of six grassland bird species, northcentral Montana, 1998–2001. The first two functions accounted for over 88% of the total discriminating power of the DFA. Dominant habitat variables are presented in order of potency index.

Variable[a]/function	DF I	DF II	Potency index
Visual obstruction-nest	0.746	−0.186	0.335
Clubmoss cover	−0.697	−0.307	0.310
Litter depth	0.629	0.270	0.251
Visual obstruction-plot	0.540	0.310	0.195
Grass cover	0.538	0.211	0.184
Vertical density-plot	0.537	0.183	0.178
Plant height-plot	0.427	0.072	0.109
Litter cover	0.389	0.170	0.097
Western wheatgrass-nest	0.299	0.382	0.090
Plant height-nest	0.329	−0.265	0.081
Vertical density-nest	0.275	−0.104	0.052
Blue grama-nest	−0.182	−0.211	0.031
Needle-and-thread-nest	−0.187	−0.149	0.026
Forb cover	−0.147	−0.112	0.020
Cactus cover	−0.125	0.108	0.015
Rock cover	−0.110	−0.069	0.009
Bare ground cover	−0.098	0.087	0.008
% of variance	55.6	33.2	
Canonical correlation	0.654	0.555	
P	0.000	0.000	

[a] Nest refers to variable measured at nest; plot refers to variables measured within 5-m radius circular plot centered on nest.

species. Conversely, none of the Sprague's Pipit and only 4.8% of Grasshopper Sparrow nests were accurately classified.

Temporal variation.—Adequate sample sizes enabled us to explore between-year variation in nest site selection for Savannah Sparrows and Chestnut-collared Longspurs (1998–2001). Among random plots, mean vegetation height (R^2 = 0.533) and vertical vegetation density at the patch level (R^2 = 0.459) showed the greatest annual variation, while litter (R^2 = 0.107) and forb cover (R^2 = 0.135) varied the least. Annual variation in nest site characteristics ranged from R^2 = 0.455 (litter cover) to 0.003 (clubmoss cover) for Savannah Sparrows, and R^2 = 0.426 (mean plant height on nest patches) to 0.035 (vertical density at the nest) for Chestnut-collared Longspurs. Strength of interactions between year and random plots for each bird species were generally weak (R^2 = 0.006–0.119) suggesting similar trends for habitat characteristics at nest and random plots (Fig. 1).

DISCUSSION

Univariate and multivariate analyses revealed similar nest site selection patterns. These patterns are best depicted at the multivariate level using a plot of group centroids on the first and second discriminant functions (Fig. 2). The dominant variables for the first function shared the common characteristic of increasing aboveground herbaceous production. This is indicated by positive associations with vertical structure (visual obstruction and vertical density), litter cover and depth, in conjunction with a negative association with clubmoss cover, which had very little vertical development (typically <3 cm in height). The second function was most associated with the presence of western wheatgrass at the nest. However, this function was difficult to interpret since no variable was strongly correlated to the function.

Sprague's Pipits used nest sites with relatively tall, vertically dense vegetation, and nest patches with greater litter cover and depth, while avoiding areas with prickly pear cactus cover. Our nest site data were consistent with findings reported by Sutter (1997) for southwestern Saskatchewan, although we found no evidence of selection against forb cover. Selection for vertical habitat characteristics by this species appears to be occurring at the scale of the nest site rather than the nest

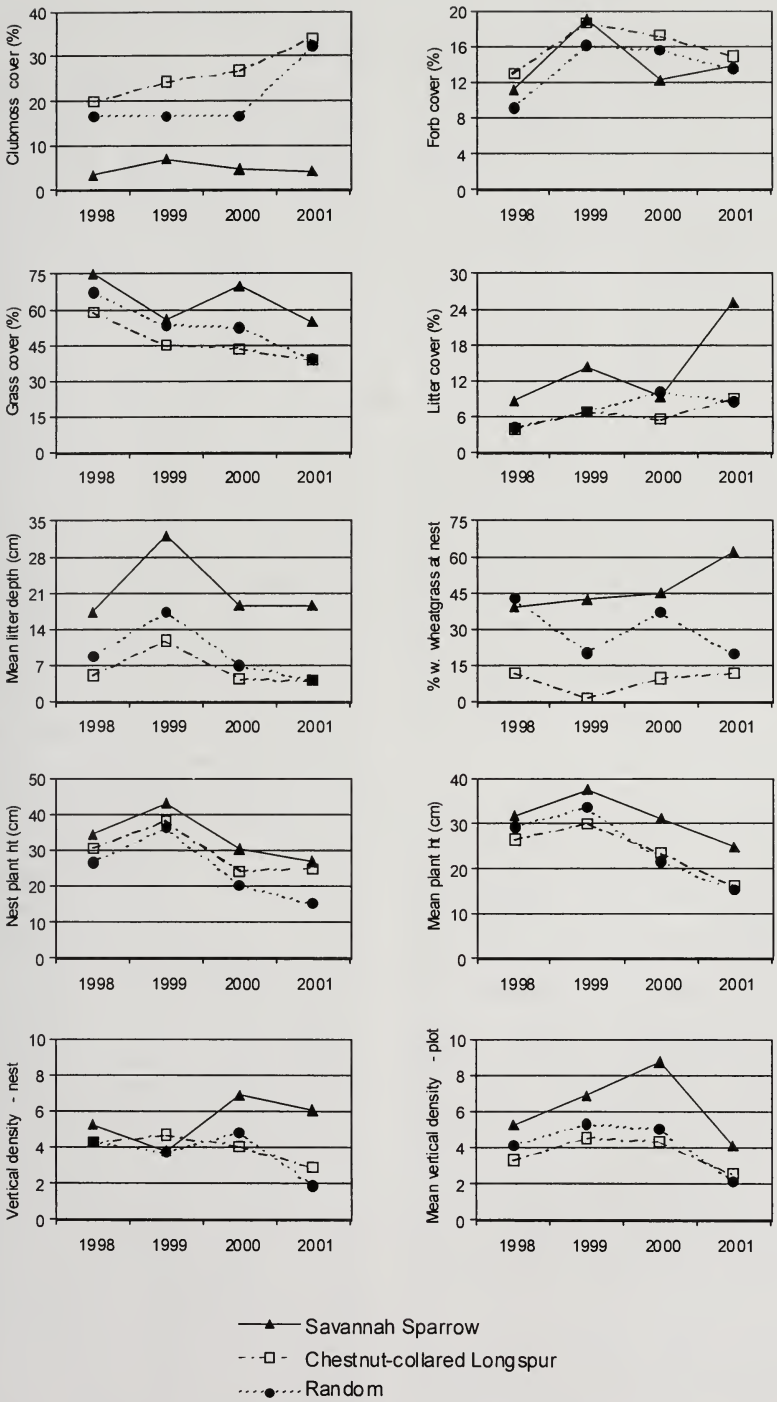

FIG. 1. Mean nest site and nest patch characteristics for Savannah Sparrows, Chestnut-collared Longspurs, and random plots in northcentral Montana.

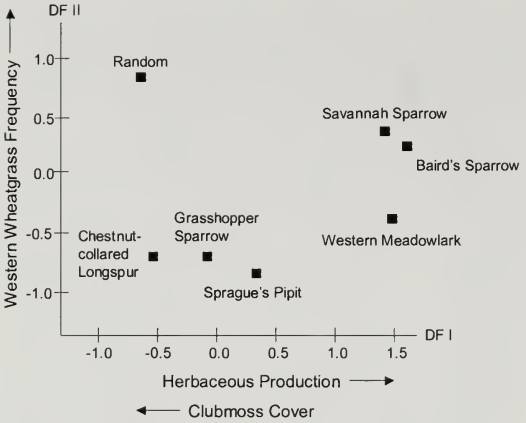

FIG. 2. Discriminant function analysis of grassland songbird nest sites, northcentral Montana, 1998–2001. Plot of group centroids for the six bird species on the first (horizontal axis) and second (vertical axis) discriminant functions. Chestnut-collared Longspurs, Grasshopper Sparrows, and Sprague's Pipits were similarly located in discriminant space, while Savannah Sparrows, Western Meadowlarks, and Baird's Sparrows formed a second, relatively cohesive group. Random plots were distinctly different from the other two groups.

patch, since these measurements were taken at both scales.

Savannah Sparrow nest patches had a well-developed litter layer, with typically little clubmoss or bare ground cover. Forb cover differed little between used and random sites, both within and among years, suggesting that this variable was merely incidental in selection. Savannah Sparrows selected several nesting habitat characteristics, but also showed great plasticity in their use, with similar trends in mean values between nest sites and random measurements. This was evident with grass cover, litter cover and depth, vertical vegetation density, and height (Fig. 2). In contrast, clubmoss cover at nest sites was consistently low across years, even though there was an apparent increase observed at random plots during 2001. This strongly suggests an avoidance of significant clubmoss cover within the nest patch. Savannah Sparrows tended to select western wheatgrass as a nesting substrate, a pattern that was relatively consistent among years, despite abrupt annual changes in the relative frequency of this grass species. This suggests that the presence of western wheatgrass may be an important factor during selection.

In contrast, Grasshopper Sparrows generally avoided western wheatgrass as a nesting substrate, using instead blue grama. Nest patches generally were devoid of any significant bare ground cover. However, clubmoss cover at nest patches was consistent with habitat availability. Grasshopper Sparrows appear to be selecting for vertical vegetative characteristics at the immediate nest site rather than at the scale of the nest patch.

Baird's Sparrows used nesting habitat with greater litter depth and taller vegetation than expected by availability, and with nest patches devoid of bare ground, which agrees with data from southern Saskatchewan (Green et al. 2002). Baird's Sparrows also selected sites with greater grass and litter cover, with vertically denser vegetation both at the nest site and nest patch, and in particular, nest patches devoid of clubmoss. Baird's Sparrows selected western wheatgrass while avoiding altogether blue grama as a nesting substrate.

Chestnut-collared Longspurs were the most abundant species on the study area, accounting for roughly half of all passerine nests, and their nest site habitat characteristics most closely resembled general habitat conditions present on the study area. However, this species tended to avoid nest sites occupied by western wheatgrass. Chestnut-collared Longspurs also used nest sites with taller and denser vegetation than were generally available, although to a much lesser degree than the other bird species. Chestnut-collared Longspurs were the only species that generally used nest patches with greater clubmoss cover than was generally available. This was evident during 1998–2000; however, selection was not observed in 2001. Forb cover also tended to be higher at nest patches than at random plots, with the difference being consistent among years, demonstrating some plasticity in habitat use. Plasticity in habitat use also was observed for grass cover and nest substrate height. Several other variables showed little difference between used and random sites within and among years, suggesting that these variables were probably not important in selection, but instead merely incidental. These included grass and litter cover, mean litter depth, vegetation obstruction at the nest patch, and ver-

tical vegetation density at the nest site and nest patch.

Western Meadowlarks were the only species that significantly avoided nest patches with high forb cover. This species generally selected nest sites and nest patches with greater visual obstruction, vertical vegetation density and height, grass cover, and litter cover and depth, while avoiding nest patches with significant clubmoss cover.

Conservation implications.—Selection for nest sites and nest patches with greater herbaceous development than random sites and patches was shown by all species. This pattern was shown most strongly by Western Meadowlarks, Baird's and Savannah sparrows. These species generally nested in patches that had little or no clubmoss cover, which was one of the most powerful discriminating variables in this analysis. Moreover, no species used clubmoss as a nesting substrate. Consequently, clubmoss may be of particular interest concerning the condition of grasslands in the northern prairie. Although clubmoss is a natural, commonly dominant component of shortgrass and mixed grass prairie (Van Dyne and Vogel 1967), it seems evident that its cover value for nesting passerines is low. Clubmoss is an evergreen, nonflowering herb that forms dense mats that rarely exceed 2.5 cm in height (Coupland 1950, Van Dyne and Vogel 1967). It is thought to be a poor competitor with other grassland associates under relatively mesic conditions, and is not an important pioneer in disturbed areas (Crane 1990). However, clubmoss is extremely drought resistant (Webster and Steeves 1964), which allows it to successfully compete during periods of below normal precipitation (Crane 1990).

Mean clubmoss cover was 21% on our study area, which is high but within the range (6–25%) reported for mixed grass prairie in western Canada (Coupland 1950). Our estimates of clubmoss cover were fairly consistent across years, until 2001 when we observed a two-fold increase in cover. Growth rate alone cannot account for this (Dolan and Taylor 1972); rather, this increase probably is an artifact of declines in mean vegetation height and grass cover observed during 2000 and 2001, where precipitation was 15 and 29% below normal, respectively. Persistent drought conditions may enable clubmoss to increase on the study area (Crane 1990).

While clubmoss was never used as a nesting substrate for any of the species in this study, little is known about its overall ecological role in native mixed grass prairie. Management actions to reduce clubmoss abundance include mechanical and fertilizer treatments (Smoliak 1965, Dolan and Taylor 1972), prescribed fire (Dix 1960, Wilson and Shay 1990), and grazing (Coupland 1950, Van Dyne and Vogel 1967, but see Brand and Goetz 1986). Grazing and fire are natural historical components of the northern mixed grass prairie (Knopf and Samson 1997), and have been mostly absent from Bowdoin National Wildlife Refuge for >25 years. Ironically, the absence of grazing and fire may have facilitated the development of denser and taller vegetation selected by most of the bird species studied here. Attempts to mimic natural disturbance patterns could impact current habitat characteristics selected by most members of this bird assemblage.

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DO RED-COCKADED WOODPECKERS SELECT CAVITY TREES BASED ON CHEMICAL COMPOSITION OF PINE RESIN?

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ABSTRACT.—We examined resin chemistry of loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines selected as cavity trees by Red-cockaded Woodpeckers (*Picoides borealis*) in eastern Texas. We sampled resin from (1) pines selected by Red-cockaded Woodpeckers that contained naturally excavated active cavities, (2) pines selected by forest biologists that contained artificially installed cavity inserts and were actively being used by Red-cockaded Woodpeckers, and (3) control pines of similar age and appearance to the active cavity trees. We hypothesized that if woodpeckers are inducing a change in resin chemistry by excavating resin wells, this change should appear in active cavity trees selected by woodpeckers and trees selected by biologists, but not in control pines. If woodpeckers are selecting pines that have specific resin chemistry, concentrations of some resin components in active cavity trees selected by the woodpeckers for natural cavity excavation should be different from both control pines and pines selected by biologists. A large diterpene acid peak containing an isopimaric-levopimaric-palustric methyl-ester mix in active natural cavity trees was approximately 20% greater than controls and 22% greater than trees with artificial cavities. None of the other eight resin chemicals differed among treatments. The activity of Red-cockaded Woodpeckers at resin wells did not appear to affect the composition of cavity tree resin. Woodpeckers, however, may select pines with specific resin chemistries for cavity trees. *Received 17 March 2003, accepted 1 August 2003.*

The Red-cockaded Woodpecker (*Picoides borealis*) nests and roosts nearly exclusively in living pines (*Pinus* spp.). Red-cockaded Woodpeckers flake off loose bark resulting in a smoother surface on the cavity tree's bole. The woodpeckers also make daily excavations at small wounds, termed resin wells, around their cavity entrance and on the bole of their cavity tree from which resin flows down the tree (Ligon 1970). These behaviors result in a resin barrier that serves as an effective defense against rat snakes (*Elaphe* spp.) if the cavity tree can produce adequate resin (Jackson 1974, Rudolph et al. 1990). Rat snakes regularly attempt to climb Red-cockaded Woodpecker nest trees and are known to prey on Red-cockaded Woodpeckers when the resin barrier is inadequate (Jackson 1978a, Neal et al. 1993).

Red-cockaded Woodpeckers make a substantial investment in time and energy when excavating a cavity (Conner and Rudolph 1995), and characteristics used to select cavity trees affect the rate of cavity excavation. Red-cockaded Woodpeckers select pines that have thin layers of sapwood and large diameters of heartwood (Conner et al. 1994), as well as pines that have had their heartwood softened by fungal decay from *Phellinus pini* infections (Jackson 1977, Conner and Locke 1982, Hooper et al. 1991) because cavities can be more quickly excavated in such pines (Conner et al. 2001).

Red-cockaded Woodpeckers also select cavity trees based on the ability of pines to produce resin (Conner et al. 1998a), which affects the defense of the cavity. The breeding male woodpecker selects the cavity tree that produces the most resin for his roost tree, which usually becomes the woodpecker group's nest tree during spring. Cavity trees producing higher yields of resin at resin wells likely provide better barriers against rat snakes, enhancing the probability of survival of the breeding male and his offspring (Conner et al. 1998a). Presumably, the woodpeckers either taste the resin or sense the viscosity of the resin early in the process of excavating a cavity and abandon the tree if they do not detect the proper resin composition. If the cavity is human made (artificial), the tasting-sensing stage may be circumvented, and the woodpeckers use this convenient resource be-

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cause it requires little or no time-energy investment in excavation, and the availability of suitable pines for cavity excavation is often low.

Pine resin (oleoresin) is a complex mixture of resin acids (diterpenes) and other chemicals dissolved in monoterpene solvents (Zinkel et al. 1971, Hodges et al. 1979). Pine resin, which the woodpecker uses to create a barrier against rat snakes, serves as the pine's primary defense against bark beetle infestation (Wahlenberg 1946, Hodges et al. 1977, Conner et al. 1998a). Red-cockaded Woodpecker cavity trees in eastern Texas, especially active cavity trees, are regularly attacked and killed by southern pine beetles (*Dendroctonus frontalis*) and occasionally by various species of engraver beetles (*Ips* spp.; Conner et al. 1991, Conner and Rudolph 1995, Rudolph and Conner 1995). High resin flow rate and total production (yield), along with a fast crystallization rate if flow rate is high, are known to favorably influence the pine's ability to physically repel a bark beetle attack (Wahlenberg 1946, Hodges et al. 1979). In addition, Hayes et al. (1994a) suggest that 4-allylanisole, a component of pine oleoresin, may serve to repel bark beetles.

Although the adhesive properties of pine resin alone may serve as the deterrent to rat snakes attempting to climb Red-cockaded Woodpecker cavity trees (Rudolph et al. 1990), repellent properties of the chemical components of pine resin also may serve this purpose (Jackson 1974). The monoterpene limonene is known to be toxic to bark beetles (Tomlin et al. 2000) and may have a similar effect on rat snakes. Thus, similar to their selection of pines for cavity excavation that have high resin yields, thin sapwood, large diameters of heartwood, and decayed heartwood, Red-cockaded Woodpeckers also may use specific resin chemistries as a selection criterion. An additional possibility is that daily excavation at resin wells on active cavity trees induces a wound response in the pine that alters resin chemistry by affecting the concentrations of various resin acid components. Wound response in pines usually involves increased resin flow volume (Ruel et al. 1998), whereas resin chemical composition normally is considered a function of the pine's genotype (Trapp and Croteau 2001). However, short term wound response in grand firs (*Abies grandis*) can involve a moderate increase in monoterpene concentration and a slight increase in diterpene concentration (Steele et al. 1998, Trapp and Croteau 2001).

We examined resin chemistry in active Red-cockaded Woodpecker cavity trees in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines in eastern Texas. We sampled resin from (1) pines selected by Red-cockaded Woodpeckers that contained naturally excavated cavities in active cavity trees, (2) pines selected by forest biologists that contained artificially installed cavity inserts and were actively being used by Red-cockaded Woodpeckers, and (3) control pines of similar age and appearance to the active cavity trees. If Red-cockaded Woodpeckers are inducing a change in pine resin chemistry by daily excavation at resin wells, this change should appear in active cavity trees which have been selected by woodpeckers for naturally excavated cavities, as well as in active cavity trees that have been selected by biologists for artificial insert installation, but not in control pines. If Red-cockaded Woodpeckers are selecting pines for cavity trees that have specific resin chemistry, concentrations of some resin components in active cavity trees selected by the woodpeckers for natural cavity excavation should be different from both control pines and pines selected by biologists that contain active cavity inserts.

METHODS

We used increment borers to collect xylem wood tissue and the resin it contained from Red-cockaded Woodpecker cavity trees in loblolly and shortleaf pines on shrink-swell soils on the northern portion of the Angelina National Forest (62,423 ha; 31° 15′ N, 94° 15′ W) in eastern Texas. A small subpopulation of Red-cockaded Woodpeckers occurs on this portion of the national forest (Conner and Rudolph 1989). We used woodpecker activity at resin wells, amount of bark scaling, and condition of the cavity entrance as indicators of tree status (see Jackson 1977, 1978b).

We sampled a total of 52 pines (36 loblolly and 16 shortleaf pines) each month during August and September 1997, including 13 active naturally excavated cavity trees, 13 active cavity trees that contained one artificial cavity

insert, and 26 control pines of similar age and general appearance to the active cavity trees. Two cores (0.5 cm diameter by 3 cm long) of xylem tissue were extracted at breast height from opposite sides of the outermost xylem rings of each pine. Both xylem core samples removed from each pine were immediately placed in foil-sealed scintillation vials in the field that were filled with 10 ml of pentane containing 0.2 mg of the internal standard tetradecane. The lids were securely tightened and the vials placed on ice in insulated coolers for transport back to the laboratory; samples were maintained in explosion-proof freezers until processed.

We analyzed terpenoid components of the resin samples using a Varian 3400 gas chromatograph with flame ionization detector. Components were separated on a J&W Scientific DB-5 column (30 m length × 0.52 mm internal diameter) using a thermal gradient program (initial temperature 70° C maintained for 5 min, increasing to 250° C by 6°/min and held for 10 min). The injector port was maintained at 260° C and the detector at 280° C; peaks were integrated using Varian ChemStar software on a PC (Varian, Inc. 1995). Samples were prepared for chromatographic analysis using a modified method of Lewinsohn et al. (1993), which allows the simultaneous analysis of mono- and diterpenoids of conifer oleoresin. Approximately 48 h prior to sample preparation, 5 ml of MTBE (methyl tert butyl ether) containing 0.25 mg of tricosanoic acid (internal standard) were added to the pentane-containing sample vials and allowed to further extract at room temperature. The mixture was then evaporated to 2.5 ml under N_2 gas and split into two 1.0-ml aliquots: one processed for monoterpenes and the other for diterpene acids. Diterpenes were esterified using TMS-diazomethane (Aldrich Chemical Co.) because it is commercially available and more stable than lab-generated diazomethane. After processing, the two fractions were recombined, further concentrated to approximately 300 ml, and analyzed. Monoterpene peaks were quantified against tetradecane, and diterpene resin methyl esters were quantified against the methyl ester of tricosanoic acid.

We identified individual peaks by comparison with published peak retention times (Hayes et al. 1994b) under replicated chromatographic conditions and confirmed them by GC-mass spectra produced from a single sample that exhibited all peaks being quantified. Mass spectra were produced using a Varian 3400GC with a 30-m DB-5 column coupled to a Saturn 3 mass detector under chromatographic conditions similar to those used for the quantitative analysis. Total terpenoid, total monoterpene, total diterpene resin acid yields, and the concentration of individual terpene components were statistically analyzed using StatView ver. 4.5 (SAS Institute, Inc. 1998). We tested all data for normality and homogeneity of variance. We pooled data across months because no monthly differences were detected in an initial two-way ANOVA design (treatment × month), and tree types (natural cavity, artificial cavity, and control) were compared subsequently with a one-way ANOVA followed by a Tukey's multiple comparison test if significant differences among means were detected. Under situations where the assumptions of parametric statistical tests were not met, data were log transformed ($\log_{x+1}$). A two-way ANOVA design (treatment × tree species) used to explore possible differences in production of specific resin components between tree species detected a difference only for α-pinene (Table 1).

RESULTS

Seven volatile monoterpene peaks, including α-pinene, β-pinene, limonene, 4-allylanisole, and three unknown smaller peaks were identified and quantified. Five diterpene methyl-ester peaks, including pimaric acid, isopimaric-levopimaric-palustric acids (quantified as a single large unresolved peak due to poor separation on the DB-5 column), dehydroabietic acid, abietic acid, and neoabietic acid also were identified and quantified. We detected no significant differences in total volatile monoterpene or total diterpene acid contents among the three treatments (Table 1). We compared individual peaks across the three treatment levels; likewise, no significant differences were seen for α- or β-pinene, limonene, or 4-allylanisole. However, the large diterpene acid peak containing the isopimaric-levopimaric-palustric methyl-ester mix did show a significant difference among the three treatment levels (Table 1), with levels found within the active natural cavity trees being

TABLE 1. Amounts of monoterpenes and diterpenes (means ± SE, mg/two-core sample) measured from increment cores extracted during August and September 1997 from active naturally excavated and active artificial insert Red-cockaded Woodpecker cavity trees and morphologically similar control pines on the Angelina National Forest in eastern Texas. Red-cockaded Woodpeckers selected pines with higher iso-levo-palustric acid levels. Means for all components except α-pinene were compared with a one-way ANOVA (df = 2, 49).

Resin chemicals	Artificial cavity trees (n = 13)	Natural cavity trees (n = 13)	Control pines (n = 26)	F	P
Monoterpenes					
α-pinene[a]	0.283 ± 0.034	0.373 ± 0.079	0.281 ± 0.026	0.71	0.982[a]
β-pinene	0.192 ± 0.021	0.232 ± 0.065	0.204 ± 0.017	0.11	0.900
Limonene	0.294 ± 0.035	0.244 ± 0.040	0.252 ± 0.028	0.65	0.524
4-allylanisole	0.501 ± 0.030	0.451 ± 0.052	0.468 ± 0.033	0.54	0.582
Total monoterpenes	1.390 ± 0.112	1.382 ± 0.230	1.295 ± 0.088	0.27	0.764
Diterpene resin methyl-esters					
Pimaric acid	0.275 ± 0.028	0.305 ± 0.030	0.279 ± 0.021	0.35	0.705
Iso-levo-palustric acids	1.938 ± 0.114	2.482 ± 0.206	1.992 ± 0.127	3.50	0.034
Dihydroabietic acid	0.218 ± 0.054	0.227 ± 0.038	0.199 ± 0.020	0.16	0.855
Abietic acid	0.295 ± 0.036	0.310 ± 0.050	0.388 ± 0.039	2.04	0.136
Neoabietic acid	0.533 ± 0.046	0.612 ± 0.043	0.615 ± 0.029	1.73	0.183
Total diterpene methyl-esters	3.259 ± 0.193	3.936 ± 0.278	3.476 ± 0.178	2.14	0.123

[a] F and P values from two-way ANOVA (treatment × tree species) for α-pinene only; see methods and results.

20% greater than controls (Tukey's P = 0.043) and 22% greater than trees with artificial cavities (Tukey's P = 0.066). We detected no difference between trees with artificial cavities and control pines (Tukey's $P > 0.99$). There was no significant interaction between treatment and month in the initial two-way ANOVA for the large diterpene peak. We found no significant differences in any of the terpenoid measures (volatiles, resin acids, or total terpenoid content) between the sampling months (August and September).

Loblolly pines produced significantly more α-pinene than did shortleaf pines ($F_{1,49}$ = 16.32, $P < 0.0001$). The two-way ANOVA design (cavity tree type × tree species) detected no significant differences among treatments (cavity types and control) for α-pinene concentrations (Table 1). There was no significant interaction between treatment and tree species ($F_{2,49}$ = 1.79, P = 0.17). We did not detect a difference between tree species for any of the other resin components.

DISCUSSION

Daily excavation at resin wells coats Red-cockaded Woodpecker cavity trees with fresh pine resin, producing a constant "wick" of resin volatiles that evaporate and diffuse from the trees. Active maintenance of resin wells by Red-cockaded Woodpeckers may induce and maintain elevated chemical defenses in trees. Under this scenario, induction could actually enhance the short term resistance of trees to beetle attack and infestation (defenses are already mobilized and wound response resin is being produced; Ruel et al. 1998), but could lower the long term resistance by depleting carbohydrate stores over time that could otherwise be used to mount an effective defensive response to a future beetle attack. However, in this study, the activity of Red-cockaded Woodpeckers at resin wells did not appear to affect the terpene yield (concentration) or composition of cavity tree resin, and argues against the idea of induced terpene defenses. We found that active cavity trees with artificial cavity inserts had the same terpene yields and composition as the control trees.

In contrast, the proportion of isopimaric-levopimaric-palustric resin acids in the oleoresin of Red-cockaded Woodpecker-selected active cavity trees was greater than that found in either the control or active artificial cavity trees. These data suggest that Red-cockaded Woodpeckers may use biochemical information, in addition to other cavity tree selection factors, as selection criteria for determining suitable cavity trees. The chemical components of the resin in pines selected by woodpeckers may have enhanced properties that maintain resin stickiness, which in turn limits

the ability of rat snakes to gain access to the nest cavity. Alternatively, woodpecker-selected cavity trees may contain higher concentrations of specific diterpene resin acids that are distasteful or toxic to rat snakes and likewise serve to inhibit rat snake climbing and thereby nest predation. Although diterpenes affect resin viscosity, the complete effect of these diterpene resin acids on resin stickiness and toxicity to rat snakes is poorly understood. Limonene, which is one of the most toxic monoterpenes to bark beetles (Coyne and Lott 1976, Raffa and Berryman 1982, Tomlin et al. 2000), was not present in significantly higher levels in cavity trees selected or used by Red-cockaded Woodpeckers. An additional possibility is that Red-cockaded Woodpeckers use resin characteristics to help detect presence of red heart fungus.

Previous research has suggested that the monoterpene 4-allylanisole in pine resin serves as a repellent to southern pine beetles (Hayes and Strom 1994, Hayes et al. 1994a). Because loblolly and shortleaf pine Red-cockaded Woodpecker cavity trees are regularly infested and killed by southern pine beetles (Conner et al. 1991, 1998b; Conner and Rudolph 1995), we expected to find lower levels of 4-allylanisole in active cavity trees that receive daily wounding from woodpeckers excavating resin wells than in control pines. This was not the case, suggesting that factors other than 4-allylanisole levels, such as the yield of resin from cavity trees (Hodges et al. 1979, Conner et al. 2001), influence cavity tree vulnerability to southern pine beetles.

In present day forest landscapes it may not be possible to obtain a precise determination of Red-cockaded Woodpecker cavity tree preference. Cavity trees currently used by Red-cockaded Woodpeckers and those selected by biologists for cavity insert installation may not provide the resin characteristics fully preferred by Red-cockaded Woodpeckers because they represent a truncated age distribution and an artifact of what was left after the removal of old growth pine forests in the South between 1880 and 1930 (Conner and O'Halloran 1987). However, resin chemistry is controlled primarily by tree genetics (Trapp and Croteau 2001) and likely is not affected by the truncated pine age distribution present throughout the South.

A more precise separation of resin chemicals within the large diterpene peak we detected and a better comprehension of the physical chemistry and toxicity of each resin component also are needed before a more complete understanding of Red-cockaded Woodpecker cavity tree selection can be achieved. Additional research is needed to evaluate resin chemistry in longleaf pines (*Pinus palustris*). Longleaf pines appear to be the preferred pine species for Red-cockaded Woodpecker cavity trees (Conner et al. 2001), and are known to produce greater yields of resin than either loblolly or shortleaf pines (Hodges et al. 1977, Conner et al. 1998a). Red-cockaded Woodpecker selection of pines with specific resin chemistries may be more pronounced in longleaf pine than in other pine species.

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AN EXPERIMENTAL TEST OF THE CONCEALMENT HYPOTHESIS USING AMERICAN GOLDFINCH NESTS

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ABSTRACT.—I conducted a vegetation removal experiment using American Goldfinch (*Carduelis tristis*) nests to test the hypothesis that predation rates vary with concealment in old field habitats in eastcentral Illinois. Daily predation rates were 0.05 for manipulated nests and 0.04 for control nests. Although manipulated nests were much less concealed than control nests, the probability of predation did not differ significantly between treatments or years. Logistic regression models indicated that nests initiated earlier in the breeding season had a greater probability of predation than nests initiated later in the breeding season. These results indicate that time of breeding season may be more important than concealment in explaining probability of predation of American Goldfinch nests in this old field system. *Received 20 February 2003, accepted 4 June 2003.*

Since predation is the major cause of nest failure for a wide range of bird species (Ricklefs 1969), identifying factors that affect the probability of predation can provide important insight concerning conservation strategies for breeding birds. Numerous studies have attempted to identify characteristics at the nest site that may reduce the probability of predation (reviewed in Martin 1992, Burhans and Thompson 1998). Many have focused on nest concealment, hypothesizing that predation rates vary with concealment and their results differ among species and habitats. Most studies used natural variation in concealment, but two (Bengston 1972, Howlett and Stutchbury 1996) tested the hypothesis by experimentally manipulating the amount of vegetation surrounding the nest. Bengston (1972) found a difference in predation rates between duck nests (genera *Aythya* and *Anas*, and tribe Mergini) where vegetation had been removed and control nests located in marsh habitats in Iceland. Howlett and Stutchbury (1996) did not find a difference in predation rates between Hooded Warbler (*Wilsonia citrina*) nests where vegetation had been removed and control nests located in mature deciduous forests in Pennsylvania.

I used experimental vegetation removal to test the hypothesis that predation rates of American Goldfinch (*Carduelis tristis*) nests vary with concealment, and predicted that manipulated nests would be depredated at a greater rate than control nests. American Goldfinches build open cup nests and are common in old fields and flood plains characteristic of early successional growth, but also use cultivated lands, roadsides, orchards, and gardens (Middleton 1993). My study of American Goldfinch nests increases the number of species and habitats (and the associated predators) examined by experimental vegetation removal, and thus provides further understanding of the effects of concealment on predation risk.

METHODS

Study area.—I conducted this study in eastcentral Illinois on two sites during the 1996 and 1997 breeding seasons. One site is a 77-ha area of the Middle Fork River Forest Preserve (40° 22′ N, 87° 57′ W). This preserve includes approximately 619 ha along the Middle Fork of the Vermilion River. The other site is a 73-ha area of the former Chanute Air Force Base (44° 17′ N, 88° 08′ W). This public use area includes approximately 860 ha along the Salt Fork of the Vermilion River. Study sites had been abandoned 7–9 years prior to the study and previously were used for farming, livestock grazing, and recreational activities. Study sites were located in a predominantly agricultural landscape; row crop agriculture (primarily corn and soybeans) covers 75% of the land area in eastcentral Illinois (Mankin and Warner 1997). Bottomland forests were dominated by silver maple (*Acer saccharinum*), American sycamore (*Platanus occidentalis*), and black walnut (*Juglans nigra*). Open habitats, including old fields, prai-

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rie restorations, croplands, and public areas (campgrounds, picnic pavilions, and parking lots) were dominated by oaks (*Quercus* spp.), hawthorns (*Craetagus* spp.), and plums (*Prunus* spp.), with herbaceous cover of goldenrod (*Solidago* spp.), thistle (*Cirsium* spp.), and big blue stem (*Andropogon gerardi*).

Nest searching and monitoring.—I conducted nest searches once every 4 days from July through September. I systematically traversed each study site and used behavioral cues to locate nests. Nest locations were marked at distances at least 5 m from the nest with plastic flagging. I monitored nests every 3–4 days during the beginning of the nest cycle and daily as hatching and fledging dates approached. For each visit I recorded date of visit and occurrences of parasitism and predation.

I considered a nest successful if it fledged at least 1 host young. I looked for confirmation of fledging by sighting nestlings, listening for nestling begging calls, and by sighting parents carrying food or scolding near the nest. I attributed nest failure to unknown causes when nest contents remained unchanged and adults were not present during at least three subsequent visits. I attributed nest failure to Brown-headed Cowbird (*Molothrus ater*) parasitism after a cowbird egg was deposited in the nest and adults were not present during at least three subsequent visits. I attributed nest failure to predation if they were empty prior to the expected date of fledging and there were no signs of fledging, cowbird parasitism, or failure due to unknown cause.

Nest site measurements.—I measured height of nest from ground to base of nest and recorded species of nest tree (or shrub). I scored concealment using methods outlined in Holway (1991). I estimated percentage of the nest concealed to the nearest 20% at 45 degree compass intervals (N, NE, E, SE, S, SW, W, NW) 1 m from the nest at three levels: ground, nest height, and 1.5 m above ground. Also, I made one estimate from directly above the nest at a height of 1 m. I calculated mean concealment which ranged from 0% for no concealment to 100% for a completely hidden nest at each of the three levels and overall concealment (mean of the 25 estimates) for analyses.

Experimental vegetation removal.—I paired nests that were active at the same time, located on the same study site, and in the early incubation stage of the nest cycle. Initial concealment was greater than 50% at all three levels. I randomly assigned one nest in each pair to the manipulated treatment.

I followed a vegetation removal protocol similar to that outlined in Howlett and Stutchbury (1996). Using hand-held pruning shears, I clipped vegetation from within a 1-m radius of the nest. To control for disturbance, I simulated this treatment at the control nest on the same day by sorting through the vegetation as if I was actually going to remove it. The simulation lasted 25 minutes, approximately the same time required to complete an actual manipulation. I estimated concealment for manipulated nests immediately following vegetation removal and again for both manipulated and control nests within one day after they became inactive.

Data analyses.—I excluded from analyses all nests that failed for any reason other than predation. I calculated daily predation rates by the Mayfield method (Mayfield 1961, 1975). I used program MICROMORT (Heisey and Fuller 1985) to calculate daily predation rates and 95% confidence intervals (CI) for each year, site, and treatment and to calculate likelihood values for models with and without year and treatment effects. I assumed that daily survival was constant throughout the nest cycle (Mayfield 1975) and calculated Mayfield estimated interval nest success as the daily survival rate raised to the length of the entire nest cycle (Middleton 1993). I compared mean daily predation rates and 95% CIs of manipulated and control nests. I compared survival models with and without year and treatment effects using log likelihood ratio tests.

I used multivariate logistic regression to examine the effects of nest site factors and time of breeding season on the probability of predation. Although logistic regression does not correct for the exposure period of individual nests, the nests used in this study were located during building or during egg laying, which minimizes the potential for this bias. Candidate variables for the logistic regression models included concealment at ground level, nest height, 1.5 m above ground, and 1 m directly above the nest, and overall concealment; date

of clutch initiation; and nest height. I selected these variables because results of previous studies suggest they may be important in explaining predation of songbird nests (Thompson and Nolan 1973, Martin 1992, Schaub et al. 1992, Filliater et al. 1994, Burhans and Thompson 1998). I used the best subsets selection method (SAS Institute, Inc. 1995) to evaluate all possible models created from the set of candidate variables. I compared these models with the log likelihood statistic, R^2, P values of the overall model, and the significance of the variables that were included. When appropriate, I used a log likelihood ratio test to evaluate which of the models was most suitable for explaining probability of predation.

RESULTS

I located 103 American Goldfinch nests during the two breeding seasons, but only 22 (11 manipulated and 11 control) nests in 1996 and 46 (23 manipulated and 23 control) nests in 1997 were eligible for analysis. The major cause of nest failure was predation, 45 (66%) of these 68 nests were depredated. Two nests (3%) were abandoned following parasitism by the Brown-headed Cowbird and one nest (1%) was abandoned for unknown reasons.

Mean overall concealment (95% CI) was 73.6% (69.4–77.7%) in 1996 and 74.8% (72.5–77.0%) in 1997. Before vegetation removal, mean concealment of control and treatment nests was similar for all five concealment measurements (mean difference, 95% CI; ground level: 2.5%, −4.3–9.3%; nest level: 0.1%, −4.6–4.7%; 1.5-m level: 4.6%, −2.3–11.5%; above nest: 0.6%, −6.0–7.2%; overall: 1.3%, −2.8–5.3%). After vegetation was removed, mean concealment of manipulated nests was much less than that of control nests for all five concealment measurements (mean difference, 95% CI; ground level: 46.2%, 40.3–52.1%; nest level: 40.6%, 35.9–45.4%; 1.5-m level: 44.2%, 38.5–50.0%; above nest: 55.3%, 49.8–60.8%; overall: 44.3%, 40.7–48.0%).

The overall daily predation rate (95% CI) was 0.04 (0.02–0.07) or an interval nest success estimate of 37% for a 25-day nest cycle. The daily predation rate (95% CI) for nests located on the Middlefork Forest Preserve and on the former Chanute Air Force Base was

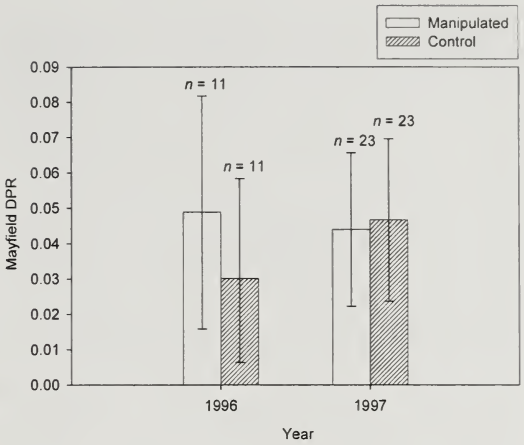

FIG. 1. Daily predation rates (mean ± 95% confidence intervals) for control and manipulated (some concealing vegetation removed) American Goldfinch nests were not significantly different in old field habitats located in eastcentral Illinois, 1996–1997.

0.04 (0.03–0.06) and 0.06 (0.03–0.08), respectively. In 1996, the daily predation rate for manipulated nests was greater than the daily predation rate for control nests; however, the CIs overlap (Fig. 1). Results from 1997 show a reverse of this trend. The daily predation rate for control nests was greater than the daily predation rate for manipulated nests; however, these CIs also overlap (Fig. 1). Likelihood ratio tests comparing models with year and treatment effects to a model with year and treatment pooled demonstrate that the probability of predation did not differ significantly between treatments ($\chi^2 = 0.10$, df = 2, $P = 0.75$) or years ($\chi^2 = 0.20$, df = 2, $P = 0.65$).

I calculated mean and 95% CIs for variables considered in the logistic regression analysis (Table 1). Nests initiated earlier in the breeding season were more likely to be depredated than nests initiated later in the breeding season (Table 2; −2 log likelihood for model = 63.00, $\chi^2 = 19.56$, df = 1, $P = 0.0001$). Nests more concealed from above were more likely to be depredated than nests less concealed from above (Table 2; −2 log likelihood for model = 59.76, $\chi^2 = 22.80$, df = 2, $P = 0.0001$). Likelihood ratio tests between these two models demonstrate that adding the variable concealment above nest to the model did not explain more variation in probability of predation than the model containing

TABLE 1. Nest site characteristics of depredated (n = 45) and nondepredated (n = 23) American Goldfinch nests were similar. Data are from eastcentral Illinois, 1996–1997.

Variable	Depredated		Nondepredated	
	Mean	95% CI	Mean	95% CI
Nest height (cm)	175	156–194	168	141–196
Concealment at ground level (%)	67	65–70	67	61–73
Concealment at nest height (%)	57	55–60	57	54–80
Concealment at 1.5 m above nest (%)	76	74–78	76	71–82
Concealment at 1 m above nest (%)	75	69–81	81	74–88
Overall concealment (%)	67	66–69	67	65–70
Date of clutch initiation	9 Aug.	7 Aug. to 10 Aug.	29 Aug.	22 Aug. to 6 Sept.

only date of initiation (Table 2; −2 log likelihood = 3.24, χ^2 = 3.24, df = 1, P = 0.072).

DISCUSSION

I found that daily predation rates for American Goldfinch nests did not differ significantly between treatments or years. The width of the 95% CIs for daily predation rates indicates a high degree of variation within the sample, so even if a real difference existed, I may not have detected it because of low statistical power (Steidl et al. 1997). For example, daily predation rates for control nests in 1997 ranged from 0.02–0.07, which represents a biologically important difference in nest success (60–12%, for the 25-day nest cycle), yet the 95% CIs for treatments in 1997 overlap.

Previous studies also have found that less concealed songbird nests are not always depredated at a greater rate than more concealed songbird nests (reviewed in Martin 1992, Burhans and Thompson 1998, Howlett and Stutchbury 1996, Braden 1999). This result may reflect cues used by predators to locate nests. If predators in this study used olfactory cues to locate nests (Henry 1969, Willis 1973, Lill 1974, Grant and Morris 1971, Eichholz and Koenig 1992, Schaub et al. 1992, Whelan et al. 1994), or depredated songbird nests incidentally (Vickery et al. 1992), my results would be expected because sight would not be important in nest detection. Burhans (1996) found no relationship between concealment and predation rates of Field Sparrow (*Spizella pusilla*) or Indigo Bunting (*Passerina cyanea*) nests in old field habitats in central Missouri. Results of video camera studies conducted at those sites found that snakes were important predators in old field habitats (Thompson et al. 1999). Robinson et al. (1999) found that fox snakes (*Elaphe vulpina*) and blue racers (*Coluber constrictor*) were more frequently associated with open habitats (old fields and grasslands) than forest habitats in eastcentral Illinois. Predation may be influenced more by nestling and parental activity (Skutch 1949, Young 1963, Perrins 1965, Nias 1986) or olfactory cues (Eichholz and Koenig 1992, Schaub et al. 1992) than by concealment if

TABLE 2. Probability of predation was negatively associated with date of clutch initiation and positively associated with concealment from 1 m directly above the nest for American Goldfinch nests (n = 68) in eastcentral Illinois, 1996–1997.

Model	Partial r^2	Parameter estimate	SE	Wald χ^2	P	Odds ratio
Model 1[a]	0.6					
Intercept		19.03	5.08	14.04	0.0002	—
Date of clutch initiation		−0.08	0.02	13.18	0.0003	0.93
Model 2[b]	0.29					
Intercept		17.70	5.10	12.04	0.0005	—
Date of clutch initiation		−0.08	0.02	12.38	0.0003	0.93
Visibility 1 m above nest		0.02	0.01	3.06	0.0800	1.02

[a] −2 log likelihood for intercept and covariates = 63.00; χ^2 = 19.56, P = 0.0001. Maximum rescaled R^2 = 0.36.
[b] −2 log likelihood for intercept and covariates = 59.76, χ^2 = 22.80, P = 0.0001. Maximum rescaled R^2 = 0.41.

snakes are dominant predators in open habitats.

Other nest site factors as well as local scale factors can be important determinants of nest success (reviewed in Martin 1992, 1993; Paton 1994; Andren 1995), but results of studies examining these relationships vary among species, habitats, and regions. This variation may exist because smaller spatial scale effects are constrained by processes operating at larger spatial scales (Donovan et al. 1997, Hartley and Hunter 1998, Thompson et al. 2002). In the midwestern United States, predation rates are negatively correlated with forest fragmentation at the landscape scale (Robinson et al. 1995). Furthermore, many species of potential nest predators are abundant and widespread in these highly fragmented, predominantly agricultural landscapes (Andren 1992, Pedlar et al. 1997, Heske et al. 1999, Dijak and Thompson 2000, Chalfoun et al. 2002). The surrounding agricultural landscape likely provides additional food sources for nest predators, which may increase their abundance throughout the landscape (Andren 1995, Marzluff et al. 1998, Dijak and Thompson 2000). Perhaps my result that predation rates did not vary with concealment was because the highly fragmented landscape may be saturated with nest predators, thus constraining the ability to detect any concealment effect.

Logistic regression models indicated that predation decreased as the breeding season progressed. Variation in predation rates during the breeding season may reflect changes in the activity patterns of the predator community or in the availability of alternate prey (Thompson and Nolan 1973). Robinson et al. (1999) found that mammalian predators, particularly raccoons (*Procyon lotor*), were abundant in eastcentral Illinois and that they moved into agricultural areas as the summer progressed and crops ripened. If generalist predators are abundant in these old field patches at the beginning of the breeding season, but increase their use of crop fields later in the breeding season, this could lead to a decline in predation rates in edge habitats as the breeding season progresses.

Concealment does not appear to affect the predation rate of American Goldfinch nests located in old field habitats in eastcentral Illinois. This result may reflect cues used by predators to locate nests or abundance patterns of predators throughout the landscape. Time of breeding season is more important than concealment in explaining probability of predation of American Goldfinch nests in this system. The importance of this factor in explaining probability of predation may reflect changes in activity patterns of predators over the breeding season. Further studies identifying nest predators, documenting the cues they use to locate nests, and examining how large scale factors affect their abundance and activity patterns during the breeding season are needed.

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DOES MALLARD CLUTCH SIZE VARY WITH LANDSCAPE COMPOSITION: A DIFFERENT VIEW

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ABSTRACT.—We report on the relationship between Mallard (*Anas platyrhynchos*) clutch size and cropland area in the landscape in western Minnesota during 1997–1999. We measured clutch size in two types of nest structures and fit a mixed-effects model to the data to examine the relationship. Our model also included covariates to control for the effects of year, nest initiation date, estimated pair numbers, and nest structure type. Unique landscapes associated with each nest (n = 134) ranged from 46.4–84.8% cropland. Clutch size was unrelated to cropland area, nest structure type, and estimated number of pairs with access to structures. Mean clutch size declined with nest initiation date early in the nesting season, but increased somewhat for nests initiated after 30 May. Clutch size also differed among years. Mean clutch size, adjusted for nest initiation date, was 11.0 ± 0.19 SE for 1997, 10.5 ± 0.19 SE for 1998, and 11.0 ± 0.19 SE for 1999. Conclusions regarding the significance of the year effect and the degree of nonlinearity due to nest initiation date were sensitive to potential clutch size outliers, but cropland area had no effect on clutch size regardless of the way we constrained clutch size. Nest parasitism by philopatric females laying in certain structures might explain the observed increase in clutch size in late nest initiations. *Received 29 June 2003, accepted 24 August 2003.*

Population size and the recruitment of young in Mallards (*Anas platyrhynchos*) are related to many factors in the landscape. Krapu et al. (1997) observed a negative relationship between the abundance of Mallard pairs and the amount of cropland in a landscape. Further, Greenwood et al. (1995) and Reynolds et al. (2001) have reported that nest success was greater in landscapes where the proportion of cropland was lower compared to that observed in landscapes with more cropland. Ball et al. (2002) recently examined the relationship between Mallard clutch size and landscape composition in North Dakota, concluding that clutches in landscapes having little cropland were larger than those in landscapes having more cropland. Their results suggest yet another way recruitment might be affected by land use. Their data came from a study of elevated nest structures that was designed to assess the influence of landscapes on Mallard use of nest structures (Artmann et al. 2001). A relationship between clutch size and landscape composition had not previously been reported for waterfowl. Thus, their results were novel and they encouraged researchers to examine the relationship in other locations and for other species of waterfowl. We initiated a study in Minnesota in 1996 that had similar objectives to those of Artmann et al. (2001). Here we report on the relationship between cropland area and Mallard clutch sizes that we observed in our study after we controlled for the effects of date of nest initiation, Mallard abundance, and nest structure type.

STUDY AREA AND METHODS

Our study area included 658 km² in southern Grant and northern Stevens counties (45° 51′ N, 96° 02′ W), Minnesota. The area is intensively cultivated and upland nesting cover for Mallards was restricted primarily to scattered tracts of mixed native and exotic grasses and forbs on state and federally managed wildlife areas, grassy fields in agricultural set-aside programs, and cover in roadside right-of-ways. Wetland drainage also has been extensive through the use of surface ditches and subsurface drainage tiles (Prince 1997). Most remaining wetlands have permanent or semi-permanent water regimes due to the consolidation of temporary and seasonal wetlands into deeper, more permanent basins. Mean Mallard breeding pair density was about 4 pairs/km² (R. Johnson unpubl. data).

We used aerial photos to select wetlands throughout the study area that were candidates for nest structure placement. We subjectively

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assessed whether a wetland had much, a moderate amount, or little cropland within about 1 km. We then selected approximately equal numbers of wetlands from each cropland class for nest structure placement. We used this strategy to assure that structures with much or little surrounding cropland would be well represented in our sample. During spring 1996, one structure was placed in each of 78 wetlands while two structures were placed in each of 16 of the largest wetlands for a total of 110 structures. Nest structure type, either a single or double nest cylinder, was assigned randomly each time a structure was erected. We inspected each structure four times each year to record nesting attempts.

We built a geographic information system (GIS) describing the land use on the study area during 1997–1999, and we used the GIS to describe landscape composition around each nesting structure within a circular area having a 3.2-km radius from the structure. This distance approximates the distance hen Mallards will travel to nesting cover (Reynolds et al. 1996). The landscape composition within each circular area described the "landscape" (32.2 km^2) surrounding each clutch. The number of Mallard pairs with access to each nest structure also was modeled with a GIS (Reynolds et al. 1996, R. Johnson unpubl. data).

We fit a mixed-effects model (PROC MIXED; SAS Institute, Inc. 2000) to test for a relationship between landscape composition and clutch size in nest structures. Fixed effects included the amount of cropland in the landscape as well as covariates for year, nest initiation date, pair numbers, and deployment type (one versus two cylinders). We included covariates for year and nest initiation date because clutch size in waterfowl can vary among years and within season (Alisauskas and Ankney 1992, Rohwer 1992). We also included covariates for pair numbers and nest structure type because nest parasitism occurred in our nest structures (Zicus et al. 2003) and the influence of different structure types was unknown.

Exploratory plots suggested a nonlinear relationship between clutch size and nest initiation date. Quadratic and cubic date effects were included in the model using orthogonal polynomials to avoid problems of collinearity (PROC IML; SAS Institute, Inc. 1989). We also centered both pair numbers and amount of cropland in the landscape (by subtracting their means from all observations) to avoid collinearity (Kleinbaum et al. 1988:208). A random subject effect (corresponding to each unique structure) was included to account for possible nonindependence among clutch sizes observed in the same structure within and among years. We used normal probability plots to validate normality assumptions of the random effect and of the within group errors (Pinheiro and Bates 2000). We assessed homogeneity of variance of the within group errors using plots of residuals versus fitted values. We tested significance of fixed effects parameters using F statistics with denominator degrees of freedom calculated using the KR method (Schaalje et al. 2002).

Clutches as large as 25 occurred in the nests that we monitored. Inspection of the distribution of observed clutch sizes suggested clutches >16 were statistical outliers. Consequently, we fit the model to clutch sizes of <17 and conducted a sensitivity analysis to assess robustness of the conclusions with respect to data sets within which clutch size was variously constrained. We also assessed robustness by fitting the model both with and without the random effect and used Akaike's Information Criterion (AIC) values to choose among competing models. The AIC value for the mixed effects model was smaller, suggesting a better fit to the data.

RESULTS

We determined clutch size for 139 nests from 1997–1999. Four clutches in single cylinder structures and one in a double cylinder structure contained >16 eggs and thus were censored from the data. Landscapes associated with each clutch varied in the percent cropland (Fig. 1) with a median of 66.1% (mean = 65.8%, range = 46.4–84.8%). We detected no relationship between clutch size and cropland area ($F_{1,55.5} = 0.10$, $P = 0.76$), structure type ($F_{1,46.1} = 0.0$, $P > 0.99$), or the number of pairs with access to a structure ($F_{1,47.5} = 0.02$, $P = 0.88$). However, nest initiation date was related to clutch size (linear date, $F_{1,123} = 65.5$, $P < 0.0001$; quadratic date, $F_{1,129} = 21.2$, $P < 0.0001$; cubic date, $F_{1,122} = 3.9$, $P = 0.051$) in a curvilinear way (Fig. 2), and

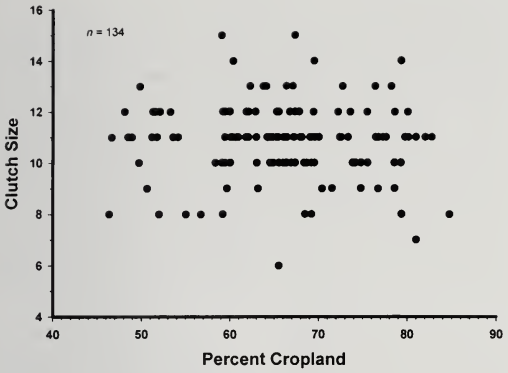

FIG. 1. There was no apparent relationship between Mallard clutch size in nest structures and percent cropland in 134 western Minnesota landscapes that were each 32.2 km² in size, 1997–1999.

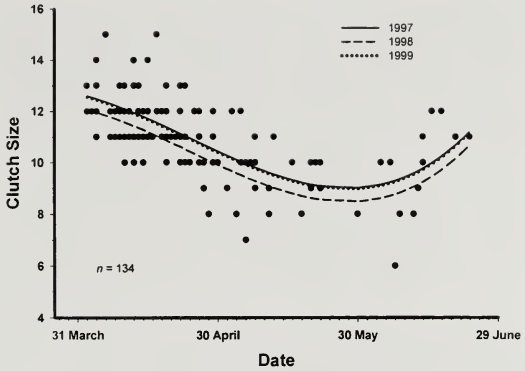

FIG. 2. Mallard clutch size in nest structures was modeled as having a curvilinear relationship to nest initiation date in western Minnesota, 1997–1999.

year had a marginally significant effect on clutch size ($F_{2,101} = 2.8$, $P = 0.065$). Mean clutch size, adjusted for nest initiation date, was 11.0 ± 0.19 SE for 1997, 10.5 ± 0.19 SE for 1998, and 11.0 ± 0.19 SE for 1999. Cropland area was not a significant predictor of clutch size regardless how we constrained clutch size in the analysis.

DISCUSSION

We detected no relationship between Mallard clutch size and landscape composition, in contrast to the findings of Ball et al. (2002). However, our study differed in several aspects from that of Ball and his coworkers. First, Mallard pair density in our study was only 30–40% of that in the North Dakota study and our nest structure density was about 10% of theirs (Ball et al. 2002). Perhaps more importantly, we defined landscapes differently. The landscape associated with each clutch in our sample was unique, extending for 3.2 km (32.2 km²) around each nest location and was intended to approximate the distance a Mallard hen would travel to nesting cover (Reynolds et al. 1996).

In contrast, Ball and his coworkers delineated 13 smaller (10.4-km²) study sites and identified them as cropland (mean = 68.9% cropland) or grassland (mean = 30.2% cropland) and classified clutches as being from either a cropland or grassland landscape. Likely, the home range of all hens would not have been entirely within their study sites, nor is it known how far individual hens traveled to reach the nest structures in the North Dakota study. Presumably, landscape composition surrounding their study sites was similar to that within each site, and thus classification of a clutch based on the amount of cropland in the entire home range of a hen would not have changed.

Further, ours was a multiyear study in which we analyzed clutch size using regression allowing the amount of cropland in the landscape associated with a clutch to vary continuously. We also included covariates for date of nest initiation, nest structure type, and estimated number of Mallard pairs with access to the nest structure to control for the effects these variables might have on clutch size. In comparison, Ball and his coworkers analyzed data from a single year comparing cropland and grassland landscapes using analysis of covariance that controlled for the effect of date of nest initiation.

We observed a few very large clutches in our data that were statistical outliers. However, we detected no relationship between clutch size and amount of cropland in the surrounding landscape regardless of how we constrained clutch size in our analysis. We suspect that the novel relationship between clutch size and landscape composition reported by Ball and his coworkers might have been an artifact of their data. Sample sizes in the North Dakota study were relatively small with only seven clutches measured from six cropland study sites and 34 nests from seven grassland sites.

As they acknowledged, larger clutches from

grassland sites might have simply reflected higher rates of nest parasitism where nests were more abundant and more easily found by parasitizing females. The mean Mallard clutch size in nests found on the ground where parasitism is unlikely has been reported to be nine eggs (Klett et al. 1986). In fact, 24% of the clutches Ball and his coworkers observed from grassland sites were >10 eggs (Ball et al. 2002: Fig. 1), which suggests a clutch size distribution that was somewhat skewed by nest parasitism. In addition to a few extremely large clutches, the pattern of parasitism in our sample seemed to be reflected by a higher frequency of 10- to 12-egg clutches over what might be expected in the absence of parasitism. Although they observed no clutches >10 eggs from their sites with abundant cropland, their sample of seven clutches was likely insufficient to truly represent the underlying clutch size distribution for structure nests in this type of landscape.

We attempted to control for parasitism in our model by including a covariate for the number of Mallard pairs having access to nest structures, but estimated pair numbers were unrelated to clutch size. This lack of association might have resulted from the fact that the pair values we relied on were estimated using a GIS model (Reynolds et al. 1996). As such, the estimates might not reflect actual pair numbers. Alternatively, conditions other than mallard abundance might influence intraspecific parasitism of Mallard nest structures and might explain our failure to detect a pair-number effect on clutch size that was separate from the cropland effect.

We observed a tendency for nests in certain nest structures to be parasitized more than others. This complicated clutch size modeling, but might explain the nonlinear trend in clutch sizes with respect to nest initiation date. For example, three of four clutches >20 eggs occurred in the same nest structure. Also, many nests initiated after 30 May were in the same nest structures that had large clutches earlier in the nesting season. Perhaps, something about these specific structures predisposed them to nest parasitism. When nests initiated after 30 May were ignored, clutch size declined at a similar rate (0.066 eggs/day) as that (0.064 eggs/day) reported by Ball et al. (2002) and that (0.054 eggs/day) observed for ground nesting Mallards in North Dakota (Krapu et al. 1983). Declining clutch size during the nesting season has been described for many birds (Klomp 1970, Rowher 1992), but increases in clutch size late in the season have not been reported previously. It seems likely that the increase we observed was a phenomenon related to nest structure philopatry by certain hens and associated intraspecific nest parasitism, and not a reflection of increased individual fecundity.

Neither our study nor that of Ball et al. (2002) was designed explicitly to investigate the influence of landscapes on clutch size, so both had limitations. Single-year studies with small sample sizes (i.e., Ball et al. 2002) are useful for posing questions and generating hypotheses, but are seldom definitive. Similarly, an argument could be made that our data were from a single landscape (i.e., a small portion of western Minnesota). We are confident that landscape composition, as we defined it, was not related to Mallard clutch size in our nest structures. However, landscape studies are inherently difficult. Levin (1992) reviewed the importance of understanding pattern and scale in ecological studies. We believe that all ecological research should be conducted with the question of landscape scale in mind. Over what scale should the landscape used by a nesting Mallard be defined? Do our results differ from those of Ball and his coworkers because of the scale at which landscapes important to Mallard hens were defined? The idea that landscape composition (or quality) could influence clutch size in waterfowl is intuitively reasonable, and Ball and his coworkers have suggested several possible mechanisms for the influence. We agree that other researchers should examine these relationships for Mallards in other landscapes and for other species in general.

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CHICK GROWTH AND PROVISIONING OF SURVIVING AND NONSURVIVING WHITE-TAILED TROPICBIRDS (*PHAETHON LEPTURUS*)

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ABSTRACT.—We examined variation in meal size, feeding frequency and daily food delivery in relation to age, nest, day, year, and weather by White-tailed Tropicbirds (*Phaethon lepturus*) using repeated weighing of chicks. We focused particularly on the differences between chicks which survived and those which died. Unsuccessful chicks became significantly lighter than successful chicks at the age of 30 days; however, some were fed until they were 60 days old. Feeding frequency and meal size differed significantly between both age classes and between surviving and nonsurviving chicks. In surviving chicks, feeding frequency remained relatively constant until chicks reached 60 days and dropped progressively thereafter. In this group, meal size was significantly lower in chicks up to 20 days old and over 70 days old than those aged 21–70 days. We found significant relationships between chick food provisioning and day, nest, and year. Feeding frequency was more important than meal size in explaining the difference in food delivery between surviving and nonsurviving chicks. This was due to much greater significant differences for feeding frequency than for meal size between surviving and nonsurviving chicks, including annual differences in feeding frequency (but not in meal size) for surviving chicks. Our study suggests that parents of unsuccessful chicks had difficulty in obtaining sufficient food for their chicks from very early on, but responded to this problem first by decreasing the feeding frequency and, later, decreasing both feeding frequency and meal size. Our study shows that parents vary in their abilities to provide optimal provisioning to their chicks. Environmental conditions determine further energetic constraints in food delivery to chicks. *Received 16 May 2003, accepted 10 October 2003.*

Pelagic seabirds are characterized by low reproductive rates, great longevity, and long incubation and chick-rearing periods, and their chicks exhibit relatively low growth rates (Ashmole 1963, Lack 1966, Warham 1990). Studies of chick provisioning in pelagic seabirds have been conducted mostly on procellariiforms and sphenisciforms in temperate and polar regions, respectively (Huin et al. 2000, Phillips and Hamer 2000 and references within). Apart from the studies of Schaffner (1990) and Schreiber (1994, 1996) on tropicbirds (*Phaethon* spp.), tropical species have received less attention, especially in describing the pattern of food delivery to chicks of all ages.

Breeding failures of entire colonies, uncommon in temperate areas (but see Schreiber 2002), occur regularly in the tropics (Ashmole 1963, Ramos et al. 2002). White-tailed Tropicbirds (*Phaethon lepturus*) have an exclusively tropical and subtropical distribution, have greater feeding frequencies (despite great variability, adults feed their chicks daily; Schaffner 1990), and show a lower productivity (0.20–0.46 chicks/breeding pair; Stonehouse 1962, Prys-Jones and Peet 1980, Phillips 1987) than other tropical seabirds, such as the Red-tailed Tropicbird (*P. rubricauda*; Schreiber 1994), and other pelagic seabirds such as the Procellariiformes (Warham 1990). These characteristics make White-tailed Tropicbirds a good subject to address the importance of feeding frequency versus meal size in the success of a nest. On Aride Island, Seychelles, where this study was conducted, the White-tailed Tropicbird breeding population has shown a 60% decrease since 1988 (Bowler et al. 2002); therefore, it is important to examine whether anomalies in chick food provisioning correlate with this decline.

We used repeated weighing of chicks to investigate temporal patterns in chick provisioning by White-tailed Tropicbirds throughout the period of nestling development. We investigated daily variation in (a) meal size (amount of food delivered by one or both parents on days that chicks were fed), (b) feeding frequency (proportion of days that chicks were fed), and (c) daily food delivery (amount of food received per day, including the value zero for days when no food was received) in relation to chick age, survivorship class (surviving versus nonsurviving chicks), nest, day,

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year, and wind speed. We examined whether meal size, feeding frequency and daily food delivery were similar among nests. The primary objective of our study was to describe seasonal and annual variations in meal size, feeding frequency, and daily food delivery of surviving and nonsurviving White-tailed Tropicbird chicks. We then discuss these parameters in relation to foraging strategies of seabirds, in particular the relationships of feeding frequency and meal size to nest success, and the influences of temperate and tropical environments.

METHODS

We studied White-tailed Tropicbirds between 2 June and 31 September of 2001 and 2002 on Aride Island, Seychelles (4° 10′ S, 55° 40′ E). We marked nests with eggs and chicks of different ages during daily routine walks along the plateau and part of the adjacent hill in June and July of 2001 and 2002. Parents brood their chicks for about 5 days after hatching and a repeated weighing protocol began when chicks were no longer being attended continuously. We obtained the weights and wing chords of a group of 10–15 chicks of known age daily at 06:00 (UTC + 4 h) during 2001. The other chicks were aged from wing length calibrated against growth of the chicks of known age. During 2002 we marked nests with chicks aged 21–65 days. We weighed 11–25 chicks every day between 2 June and 1 August, 2001 (except on 17, 22, 24, 26, 29 and 30 July), and 5–25 June 2002. We used the larger data set of 2001 in all comparisons between surviving and nonsurviving chicks. Data for 2002 was used only to compare chick food provisioning between 2001 and 2002, for surviving chicks aged 21–70 days.

In 2001, 12 chicks were weighed at 6-h intervals (06:00, 12:00, 18:00 and 00:00) during the first five days of the study. However, since only a small increment in body mass (3–7 g) was detected between 18:00 and 00:00, and that was for only three chicks <11 days old (5% of the chick days), no further chicks were weighed at 00:00 after 6 June. Schreiber (1994) also showed that Red-tailed Tropicbirds are not fed at night. Any overnight gains in body mass were omitted from the analyses. In August and September all remaining chicks were checked once or twice a week to assess whether they survived or not.

Daily feeding events were determined from the repeated weighings. Each weighing period lasted 30–40 min and chicks were always weighed in the same sequence. On six occasions chicks regurgitated food while being handled, but this was fed back to the chicks. Increases in chick mass between weighings were attributed to feeding by adults, and positive mass increments were used to estimate meal sizes, feeding frequency, and daily food delivery following established procedures (Ricklefs et al. 1985, Bolton 1995, Phillips and Hamer 2000). The sums of positive mass increments (SUM; Ricklefs 1984) between repeated 6-h weighings each day are an index of the amount of food delivered by the parents. This underestimates the amount of food delivered because chicks loose mass through respiration and excretion over this period. We estimated mass loss before and after feeding in 2001, using stepwise multiple regression (Bolton 1995, Phillips and Hamer 2000). Stepwise multiple regression was used to investigate the relationship between rates of mass loss by chicks, in the intervals before feeding and after feeding, and initial mass, chick age, and the size of meal received. The best predictions were obtained with untransformed data. The rate of mass loss prior to a feeding was significantly and independently related to both initial mass and chick age. Initial mass (g) accounted for 14.6% of the variation in mass loss (g/h) and chick age (days) accounted for 13.4%: mass loss = 0.012 (± 0.001 SE) × initial mass − 0.033 (± 0.005 SE) × age − 0.051 (± 0.212 SE); $F_{2,234}$ = 46.4, $r^2 = 0.28$, $P < 0.0001$. The rate of mass loss following a feeding was significantly and independently related to initial mass, amount of food received, and chick age, which accounted for 55%, 11% and 1% of the variation, respectively: mass loss = 0.011 (± 0.001 SE) × initial mass − 0.018 (± 0.002 SE) × meal size − 0.013 (± 0.004 SE) − 0.614 (± 0.176 SE); $F_{3,307}$ = 210.2, $r^2 = 0.67$, $P <$ 0.0001.

We used the above equations to estimate mass loss between initial and final consecutive weighing periods, assuming that the feedings occurred in the middle of the weighing period. This estimate was then used to correct SUM,

in order to determine the total amount of food delivered to the chick. The correction was applied when a positive increase in mass was detected between weighings. Therefore, very small meals delivered soon after one weighing may have been undetected, but these would be of low energetic value to the chick.

Meal size represents the amount of food, given by one or both parents, delivered on days that chicks were fed. We stress that our definition of meal size is not coincident with meals of individual parents, as measured in previous studies of White-tailed Tropicbirds (Schaffner 1990). We defined daily food delivery as the total amount of food received on a daily basis; the value zero was used for days when no food was received. We assessed the relationship of total daily food delivery, chick age, and chick mass at 06:00 on the 24-h mass changes of chicks from 06:00 to the following 06:00 (NET; Ricklefs 1984).

The weighing data represented repeated measurements from the same chicks. All analyses were done separately for surviving and nonsurviving chicks. Data on estimated meal size and estimated daily food delivery were normalized by log (x) and log (x + 1) transformation, respectively. However, for surviving chicks, results obtained with transformed and untransformed data were very similar, possibly due to the larger sample size. As the sample size for nonsurviving chicks was smaller we performed all analyses on transformed data.

We examined differences in feeding frequency among age classes with Kruskal-Wallis nonparametric analysis of variance. We used logistic regression to evaluate the relationship between chick feeding frequency (fed, not fed) and day and nest. The dependence of meal size and daily food delivery from age class, day, nest, and year was examined with one-way ANOVA. When significant differences were found, *post hoc* tests were conducted using the Tukey test (Zar 1996). For 2001, we also examined the relationship between wind speed and mean daily food delivery for surviving chicks using the Pearson correlation coefficient. We obtained daily mean wind speed for the period June to July 2001 (in knots; 1 knot = 1.85 km/h) from the meteorological station at Mahé airport, about 40 km from Aride. We assumed that these values represent the mean wind speed conditions in the area of inner Seychelles where White-tailed Tropicbirds foraged.

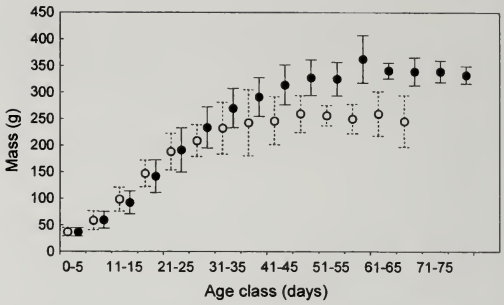

FIG. 1. Growth curves (mean ± SD) for surviving (closed circles) and nonsurviving (open circles) White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001. The number of chick-days for each age class ranged from 8–106; median = 41 for surviving chicks and 13 for nonsurviving chicks.

To test whether weighing chicks at intervals throughout the day might disturb feeding events, we compared body mass of chicks weighed at 6-h intervals to those of 10 chicks weighed once a day at 06:00, over the same period in 2001. These extra 10 chicks were interspaced with the other chicks; therefore, the 06:00 round lasted up to 55 min.

RESULTS

Chick growth.—There was no significant difference in age specific masses of frequently weighed chicks compared to chicks weighed only once a day in 2001 (ANCOVA with age as covariate, $F_{1,1768} = 0.37$, $P = 0.30$).

Changes in body mass of surviving and nonsurviving chicks in 2001 in relation to chick age are presented in Fig. 1. Chicks that survived reached a mean peak mass of 362.4 g ± 44.7 SD at the age class of 56–60 days. Mass of chicks that did not survive was similar to that of surviving chicks until 21–25 days, but thereafter the difference between the two groups increased with age (Fig. 1). Surviving chicks increased in mass at a mean rate of 7.8 g/day from hatching until 35 days, and growth slowed to 3.7 g/day from 36–60 days. From 61–80 days chicks lost mass at a mean rate of 1.5 g/day. Nonsurviving chicks gained mass at a similar rate to that of surviving chicks (mean of 7.6 g/day) until 25 days, but their growth slowed to a mean of 2.5 g/day from 26–50 days. Nonsurviving chicks lost

TABLE 1. Feeding frequency (proportion of days that chicks were fed) and meal size (amount of food delivered by one or both parents, delivered on days that chicks were fed) for surviving and nonsurviving White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001. Values are mean ± SD, *n* = number of chick-days.

Age class (days)	Feeding frequency				Meal size (g)			
	Surviving	*n*	Nonsurviving	*n*	Surviving	*n*	Nonsurviving	*n*
<10	1.00 ± 0.0[a]	16	0.86 ± 0.36[a]	21	26.9 ± 19.6[a]	16	26.0 ± 10.7[a]	18
11–20	0.96 ± 0.21[a]	90	0.88 ± 0.33[a]	50	51.0 ± 22.5[a]	86	43.8 ± 18.8[ac]	44
21–30	0.89 ± 0.32[a]	116	0.75 ± 0.43[b]	57	69.3 ± 30.4[a]	103	65.1 ± 26.7[a]	43
31–40	0.96 ± 0.93[a]	134	0.78 ± 0.42[a]	46	71.9 ± 32.8[a]	118	66.8 ± 30.2[a]	36
41–50	0.92 ± 0.27[a]	125	0.71 ± 0.46[b]	49	75.6 ± 33.3[a]	115	60.1 ± 26.4[b]	35
51–60	0.92 ± 0.27[a]	117	0.72 ± 0.45[b]	36	74.9 ± 32.4[a]	108	57.6 ± 27.0[b]	26
61–70	0.80 ± 0.40[a]	85	0.45 ± 0.51[b]	20	76.3 ± 32.1[a]	68	64.9 ± 26.1[a]	9
71–80	0.73 ± 0.45	37			54.2 ± 27.4	27		

[a,b] For each group, feeding frequency and meal size, rows sharing the same letter were not significantly different (Kruskal-Wallis and *t*-tests comparing chicks of the same age class for feeding frequency and meal size, respectively).
[c] The difference was not significant when two outliers of the surviving group were removed.

mass at a mean rate of 0.6 g/day from 51–70 days.

Feeding frequency.—The proportion of surviving chicks in 2001 that were fed each day was higher at all age classes than that of nonsurviving chicks (Table 1). The feeding frequency for surviving chicks remained relatively constant until chicks reached 60 days and decreased progressively thereafter. There were significant differences in the probability of surviving (Kruskal-Wallis $H_{7,720} = 24.8$, $P = 0.007$) and nonsurviving ($H_{6,279} = 16.3$, $P = 0.012$) chicks being fed according to age class (Table 1). For surviving chicks, those in the older age classes (>60 days) were fed less frequently than younger chicks (Table 1). For nonsurviving chicks, feeding frequency was significantly higher in chicks aged up to 20 days than for those aged 21–60 days, and higher in both these groups than in chicks aged 61–70 days. Kruskal-Wallis pairwise comparisons for each age class showed that feeding frequency differed significantly between surviving and nonsurviving chicks for all age classes over 20 days, except those aged 31–40 days (Table 1).

For chicks aged 21–70 days in 2001, there was no significant relationship between chick feeding frequency (fed, not fed) and day and nest, for both surviving (logistic regression Wald $\chi^2_1 = 2.70$, $P = 0.26$) and nonsurviving chicks ($\chi^2_1 = 4.24$, $P = 0.12$). For surviving chicks aged 21–70 days, the daily feeding frequency in 2001 was significantly higher than that in 2002 (Table 2). Overall, chicks were fed significantly more in the morning than in the afternoon during both 2001 and 2002 (58.2% and 60.1% of the feedings in the morning, respectively; $\chi^2_1 = 29.2$, $P < 0.0001$, $n = 1087$, and $\chi^2_1 = 6.7$, $P = 0.008$, $n = 173$).

Meal size.—In 2001, meal size in the surviving group was significantly lower in chicks aged up to 20 days and over 70 days than

TABLE 2. Feeding frequency (proportion of days that chicks were fed), meal size (amount of food delivered by one or both parents, delivered on days that chicks were fed) and daily food delivery (total amount of food received on a daily basis; the value zero was used for days when no food was received) for surviving White-tailed Tropicbird chicks, aged 21–70 days. Values are mean ± SD, *n* = number of chick-days. Data are from Aride Island, Seychelles.

	2001	2002	Statistic
Feeding frequency	0.89 ± 0.31 (*n* = 577)	0.80 ± 0.40 (*n* = 181)	$\chi^2_1 = 8.6$, $P = 0.003$
Meal size (g)	73.6 ± 32.1 (*n* = 511)	74.4 ± 31.0 (*n* = 145)	$F_{1,654} = 0.68$, $P = 0.410$
Food delivery (g)	65.3 ± 38.1 (*n* = 577)	59.3 ± 40.8 (*n* = 182)	$F_{1,757} = 8.23$, $P = 0.004$
Daily mass increments (NET, g)	3.25 ± 20.3 (*n* = 705)	0.81 ± 19.8 (*n* = 182)	$H_{1,885} = 1.46$, $P = 0.230$

those aged 21–70 days, but no significant difference was detected between chicks aged 11–20 and those aged 71–80 (one-way ANOVA $F_{7,632} = 16.6$, $P < 0.0001$). In 2001, meal size for nonsurviving chicks also differed significantly among age classes (one-way ANOVA $F_{6,205} = 10.2$, $P < 0.0001$). Meal size for chicks aged up to 10 days was significantly lower than in all other chicks, and meal size for chicks aged 11–20 was significantly lower than those aged 21–40 days (Table 1). Paired *t*-tests between surviving and nonsurviving chicks of each age class showed that meal size differed significantly only for chicks aged over 41 days (Table 1).

The dependence of meal size on nest was used to assess consistency in the size of meals delivered to surviving chicks aged 21–70 days (for which meal size was independent of age). This analysis showed a significant degree of variation between chicks in meal size received in 2001 ($F_{18,492} = 2.60$, $P = 0.0004$) but not in 2002 ($F_{11,133} = 1.28$, $P = 0.24$). From 18 nests in 2001, one nest (mean = 50.4 g) was different from two other nests (mean = 87.3 and 85.9). For the same age group, daily variation in meal size was significantly different in 2001 ($F_{54,456} = 1.67$, $P = 0.003$) but not in 2002 ($F_{18,126} = 1.57$, $P = 0.082$. Tukey range tests identified a significant difference between 4 July (meal size = 47.1 g) and 23 and 26 July 2001 (meal sizes of 97.3 and 93.8 g, respectively). For surviving chicks aged 21–70 days meal size did not differ significantly between 2001 and 2002 (Table 2).

For nonsurviving chicks in 2001, there was a significant association between nest and meal size ($F_{9,178} = 2.74$, $P < 0.005$), but no significant differences were found with Tukey tests. No significant association was obtained between day and meal size ($F_{52,87} = 0.87$, $P = 0.071$).

Total daily food delivery.—The mean amount of food received each day in 2001 for surviving and nonsurviving chicks in each age class is shown in Fig. 2. For surviving chicks, daily food delivery for chicks aged 11–60 differed significantly from chicks aged 71–80 ($F_{7,712} = 3.61$, $P = 0.0008$). There was no significant difference in daily food delivery among age classes for nonsurviving chicks ($F_{6,272} = 1.94$, $P = 0.074$).

For surviving chicks aged 20–70 days, total daily food delivery differed significantly among chicks ($F_{18,558} = 2.66$, $P = 0.0002$) and days ($F_{54,522} = 1.89$, $P = 0.0003$) in 2001. Two chicks (mean food delivered = 40.6 and 44.6 g) differed from seven other chicks (mean food delivered = 60.6–83.2 g). In terms of daily variation, there was a significant difference between 5 July 2001 (mean food delivered = 33.1 g) and 18 and 23 July 2001 (mean food delivered = 91.8 and 97.3 g, respectively). In 2002, total daily food delivery differed significantly among days ($F_{18,163} = 1.90$, $P = 0.020$, although no significant differences were found with the Tukey test) but not among nests ($F_{11,170} = 1.06$, $P = 0.15$).

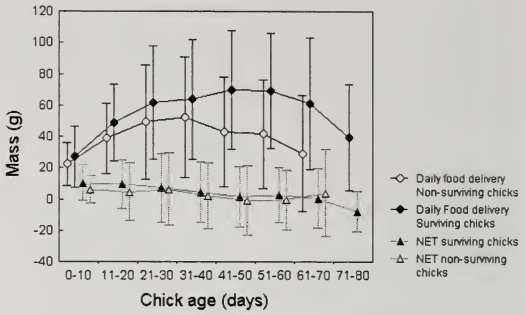

FIG. 2. Estimated daily food delivery and 24-h mass change (NET; mean ± SD) in relation to chick age for surviving and nonsurviving White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001 (n = 37–134 surviving chicks and 20–57 nonsurviving chicks).

There also was a significant relationship between nest and overall food delivery of nonsurviving chicks in 2001 ($F_{10,199} = 1.95$, $P = 0.041$). The Tukey test identified a difference between one nest (mean food delivered = 30.3 g and two others (mean food delivered = 62.8 and 63.5 g). For surviving chicks aged 21–70 days, total daily food delivery differed significantly between 2001 and 2002 (Table 2).

There was no significant correlation between mean daily food delivery and wind speed for surviving chicks aged 20–70 days in 2001 ($r = -0.19$, $P = 0.20$, $n = 54$). The relationship of day and wind speed with total daily food delivered for nonsurviving chicks was not examined due to a small sample size for each day.

Daily mass change.—Changes in daily mass increments (NET) for surviving and

nonsurviving chicks in 2001 are presented in Fig. 2. In a stepwise multiple regression, NET (in g) was significantly and independently related to daily food delivery, age, and chick mass at 06:00 according to the following equation (for both surviving and nonsurviving chicks, since equations were similar for each group): NET = 4.89 (± 0.97 SE) + 0.47 (± 0.009 SE) × daily food delivery + 0.27 (± 0.03 SE) × age − 0.16 (± 0.006 SE) × mass at 06:00 ($F_{3,900}$ = 1059.0, $P < 0.0001$, r^2 = 0.78).

Variation in daily food delivery accounted for 56% of the variation in NET and, after controlling for that, NET was greater in older chicks and lower in chicks that were initially heavier. Mean daily mass increments for surviving chicks aged 21–70 days did not vary significantly between 2001 and 2002 (Table 2).

DISCUSSION

Pattern of chick provisioning for surviving and nonsurviving chicks.—It is not surprising that chicks that died experienced a low provisioning rate that ultimately resulted in starvation and death. Feeding frequency was more important than meal size in explaining the difference in chick food delivery between surviving and nonsurviving chicks, because there were much greater differences for feeding frequency than for meal size between surviving and nonsurviving chicks. Moreover, surviving chicks showed a significant difference in feeding frequency (but not in meal size) between years. Our study shows that significantly lower feeding frequency of nonsurviving chicks occurred from the age of 20 days onwards, whereas significantly lower meal size occurred only from the age of 41 days. This means that parents of unsuccessful chicks had difficulties in finding and catching the necessary food for their chicks from very early on but responded to this problem first by decreasing the feeding frequency and later, by decreasing both feeding frequency and meal size. Thus, a reduction in the rate of increase in mass was apparent from about day 30. We found that (1) within each year nonsurviving chicks had lower performing parents, and (2) parents of surviving chicks showed a significant difference in performance between years.

In terms of the time of day that food was delivered to chicks, 58% of the feedings on Aride were before 12:00; in contrast Schaffner (1990) recorded about 90% of the meals in Puerto Rico before 12:00. Schreiber (1994) also found that 71–73% of adult feedings in Red-tailed Tropicbirds breeding on Christmas Island and Johnston Atoll, central Pacific Ocean, were delivered between 07:00 and 13:00. The fact that White-tailed Tropicbird chicks were more likely to be fed in the morning than in the afternoon at both Aride and Puerto Rico suggests that nocturnal feeding on species such as squid, which migrate to the surface at night, is important for White-tailed Tropicbirds throughout the world. Indeed, of the 14 regurgitations and prey remains obtained at nests in 2001 and 2002 on Aride, 30% had squid. Other important prey items were flying fish (Exocoetidae) and mullids (Mullidae), suggesting that prey also were captured during the day. Presumably the Aride birds foraged closer to their breeding grounds than the Caribbean birds because coastal species such as mullids were not found in the diet of Puerto Rican birds (F. C. Schaffner pers. comm.).

We found significant relationships between chick provisioning and day, nest, and year. Daily variation in chick food provisioning was rather small, i.e., it was due to an effect of meal size received on 3 of 60 days in 2001. Chick feeding frequency of surviving chicks was significantly higher in 2001 than in 2002, suggesting that food availability was higher in 2001. In fact, productivity (number of chicks fledged per pair) was slightly higher in 2001 (0.29, n = 68) than in 2002 (0.27, n = 42; unpubl. data). While surviving chicks in 2001 received food more frequently than did surviving chicks in 2002, NET values did not differ significantly between years. Presumably, lighter chicks were less costly to maintain, reduced their activity (Schreiber 1994), and/or their metabolic rates were adjusted to lower food delivery rates (Klaassen and Bech 1992). The ability to grow more slowly as a response to lowered food provisioning, and still survive, has important advantages for species, such as the White-tailed Tropicbird, that are subjected to a high degree of variability and unpredictability in collecting food resources (Navarro 1992, Schreiber 1994). However, within each age class in 2001, the NET values of surviving chicks were similar

to those of nonsurviving chicks. This suggests that underweight chicks reduced their growth to a very large extent, with a presumed progressively reduced metabolism and body temperature (Klaassen and Bech 1992), and perish only after a prolonged period of low food delivery.

The difference in food delivery to surviving chicks between years occurred at the level of feeding frequency rather than meal size. Granadeiro et al. (1998), studying Cory's Shearwater (*Calonectris diomedea*) in the Atlantic Ocean, reached a similar conclusion. Annual differences in feeding frequency, but not in meal size, seem to be a widespread phenomenon in seabirds. Energetic constraints should impose a strong selection for parents to increase the individual meal size, while reducing the number of feedings as much as possible (Schaffner 1990). Direct observations of individually marked White-tailed Tropicbird adults showed that the typical payload size carried by adults was significantly less than half of the size that they can transport. The chicks' swallowing capabilities occur before the parents' transport limits are reached, and seem to set the load carried by individual parents at a size that they can easily transport (about 40% of the maximum payload size; Schaffner 1990). Due to great spatial and temporal variation in the food supply, it is expected that feeding frequency will show greater variability than meal size (Schaffner 1990), which is what we found in our comparison between years and between surviving and nonsurviving chicks. Red-tailed Tropicbirds breeding on Johnston Atoll, central Pacific Ocean, also showed a greater variability between years in feeding frequency than in meal size (Schreiber 1994).

The low abundance and unpredictability of food resources in tropical areas often has been suggested as a reason for lower seabird productivity in the tropics (Ashmole 1963, Ramos 2000). The differences in feeding frequency and meal size between surviving and nonsurviving White-tailed Tropicbird chicks, and the lesser importance of daily variation in meal size, suggest that within a particular year, even good feeding conditions cannot mask the effect of optimal feeding frequency by parents.

Chick food provisioning: comparison with other pelagic seabirds.—Results from other studies of pelagic seabirds are similar to our results in showing smaller meals and a higher feeding frequency for very young chicks than for older chicks (Schreiber 1994, Bolton 1995, Hamer and Hill 1997, Ramos et al. 2003). Such general trends should result from a gradual increase in the overall capacity of the digestive tract (Phillips and Hamer 2000) and the swallowing capacity of chicks (Schaffner 1990). In agreement with studies of Red-tailed Tropicbirds (Schreiber 1994) and other pelagic seabirds (e.g., procellariiforms; Bolton 1995, Ramos et al. 2003), the increased demand in food requirements as chicks grew was paralleled by an increase in the amount of food consumed (for chicks aged up to 50 days in our study), but not in the daily feeding frequency. For surviving chicks of White-tailed Tropicbirds the percentage of days that chicks were fed showed little age-specific variation until chicks reached the oldest age class. Also, Schreiber (1994) observed Red-tailed Tropicbird chicks from dawn to dusk, and found that the number of feedings received per day by medium and large chicks was similar. An increase in the daily amount of food received by White-tailed Tropicbird chicks as they grew can be explained by an increase in the swallowing capacity of chicks, the meal delivery frequency of parents, and the probability of both parents returning to the nest simultaneously (the chick receives the entire meal size or none of it; thus, if both parents arrive at approximately the same time with a combined amount of food larger than the chick's swallowing capacity, the second meal will be completely lost). Tropicbirds feed their chicks with meals consisting of a combination of large and small items (Schaffner 1990, JAR pers. obs.), and the risk of wasting oversized meals is much higher than in seabirds that feed their chicks with partially digested food or with stomach oil of high calorific content (e.g., procellariforms; Phillips and Hamer 2000).

In situations of low resource availability, temperate procellariiforms deliver larger meals at a lower feeding frequency than those delivered under favorable feeding conditions (Chaurand and Weimerskirch 1994, Granadeiro et al. 1998), presumably as a compromise between feeding their chicks and maintaining their own body condition (Weimerskirch et al.

1997). We did not find evidence of this mitigating feeding behavior in White-tailed Tropicbirds because in 2002, when food presumably was less abundant than in 2001, the adults decreased the feeding frequency but did not increase the size of the meals delivered to chicks. Increasing meal size may not be an option for tropical seabirds that feed on dispersed prey such as flying fish.

Natural selection has produced White-tailed Tropicbird parents that carry an approximately optimal payload size to their chicks, imposed by mechanical and volume constraints (of which the maximum swallowing capacity of chicks is the most important) and energetic constraints such as weather, food abundance and availability, and distance of food sources from the nesting colony (Schaffner 1990). Such selection pressures seem to have fixed the meal mass at a relatively narrow size, that the adults will try to collect as quickly as possible (Schaffner 1990). Our study shows that (1) individuals vary in their abilities to provide optimal provisioning to their chicks (which is related to chick survival), and (2) environmental conditions (shown by our differences in feeding frequency between years) provide important energetic constraints for parents in provisioning their chicks. Changes in the abundance and availability of food resources due to anthropogenic influences are likely to affect the optimal provisioning of chicks, with possible negative consequences on the survival of White-tailed Tropicbird nestlings.

Although food delivery varied between years, we were unable to determine if low chick provisioning affected the entire population, and thus could account for the decline of the White-tailed Tropicbird population on Aride Island (Bowler et al. 2002). However, as White-tailed Tropicbirds breed throughout the year, chick food provisioning also should be examined during the northwest monsoon season (October to April).

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SURVIVAL AND MOVEMENT OF POSTFLEDGING JUVENILE HARLEQUIN DUCKS

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ABSTRACT.—Age specific survival and movement are important components of demography and population structure, and quantification of these rates is useful for management and conservation. However, information on the postfledging ecology of waterfowl species frequently is unavailable to managers. I studied postfledging survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia, using radio marking and capture-mark-recapture analysis of banded birds captured at coastal wintering areas. Survival of juvenile females was high, providing evidence that female winter survival may be similar among age groups. Radio-marked juvenile males were more likely to die than juvenile females, and juvenile males had lowest local survival rates of all sex-age classes. Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and at least 25% (n = 9) of radio-marked females moved >30 km from their capture location. These results were unexpected, based on previous evidence for female philopatry and theories of male-biased dispersal in waterfowl, and suggest that males and females both likely contribute to gene flow and demographic connection among populations. *Received 14 March 2003, accepted 15 November 2003.*

The immature stage has been shown to play an important role in population dynamics in some waterfowl species (Coulson 1984, Cooch and Cooke 1991). However, information on postfledging survival and movement patterns frequently are unavailable to managers. Although age ratios may provide a measure of production for hunted species (Bellrose 1980) and for species with visually identifiable first-year plumage (Smith et al. 2001, Iverson et al. 2003, Rodway et al. 2003a), age specific survival rates are needed to estimate recruitment into the breeding population (Cooch and Cooke 1991, Perrins 1991, Anderson et al. 2001). Survival rates of juveniles generally are difficult to estimate. Juveniles can be difficult to identify or capture, frequently resulting in small sample sizes. Also, survival rates often are confounded by juvenile dispersal from study areas, and dispersal can be difficult to assess without simultaneous sampling of neighboring populations (Clobert and Lebreton 1991). Thus, information on dispersal is needed to separate mortality from emigration (Lebreton et al. 1992), which is an important distinction for large scale management of populations. In addition, although much emphasis has been placed on philopatry of waterfowl to breeding areas (Anderson et al. 1992), little attention has been paid to winter philopatry and dispersal (Robertson and Cooke 1999). Because many waterfowl pair during winter, it is the movements of unpaired individuals among wintering areas that largely influence the degree of genetic structuring among populations for many species (Rockwell and Barrowclough 1987). Information on movement patterns during winter also are important to the understanding of demographic connection among wintering populations (Esler 2000).

I investigated survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) captured at wintering areas. Harlequin Ducks breed at inland streams, winter at coastal areas, show delayed maturation, pair during winter, and form long term pair bonds (Robertson and Goudie 1999). Previous analysis for a small wintering population indicated that local (or apparent) survival (the probability of surviving and returning to the study area; Lebreton et al. 1992) of juvenile and subadult males was lower than that of adults, but that local survival rates of females did not differ among age groups (Cooke et al. 2000). Assuming that differences in local survival rates of young males and females were due to differences in emigration rates and not death, these results supported theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992), and suggested that dispersal of males resulted in a considerable amount of gene flow among populations.

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My objectives were to use radio marking to estimate survival and movement of juveniles during their first winter and to allow separation of mortality from emigration, to use capture-mark-recapture (CMR) analysis to compare local survival among sex-age classes, to determine whether age specific mortality rates should be incorporated into estimates of recruitment, and to test predictions of male-biased dispersal. I chose the juvenile age class because survival and movement rates during the first year of life likely differ most from that of mature birds and because information on postfledging ecology is lacking almost entirely, not only for Harlequin Ducks, but also for other sea ducks and many waterfowl species.

METHODS

Researchers captured juvenile Harlequin Ducks at coastal wintering areas using two methods. We captured 15 juveniles among older birds in drive traps designed to capture flightless molting adults from mid-August through mid-September, 1995–1998. In addition, we specifically searched for juveniles and captured 19 of them using mist nets and decoys during the first half of September in 1999 and 2000. We captured juveniles on Hornby Island (49° 32′ N, 124° 40′ W) and on the eastern coast of Vancouver Island between Comox (49° 42′ N, 124° 52′ W) and Campbell River (49° 58′ N, 125° 12′ W) in the northern Strait of Georgia (Fig. 1), and at White Rock (49° 02′ N, 122° 51′ W) in the Lower Mainland, British Columbia. We identified juveniles by the finely vermiculated plumage on their breast, belly, and vent, their mottled yellowish legs and feet, and their dusky faces, full primaries, and notched tail feathers (Regehr et al. 2001), and sexed them by cloacal examination. We marked all captured juveniles with a U.S. Fish and Wildlife Service band on the left tarsus, and a colored, laminated plastic band uniquely engraved with two alpha numeric digits on the right tarsus. During September 2000, we also marked 15 juveniles (nine females, six males) with external radio transmitters attached mid-dorsally with subdermal wire anchors. We captured radio-marked juveniles at Hornby Island, Comox, and Willow Point (Fig. 1). Nine radios weighed 9 g each and had 2-cm wide wire

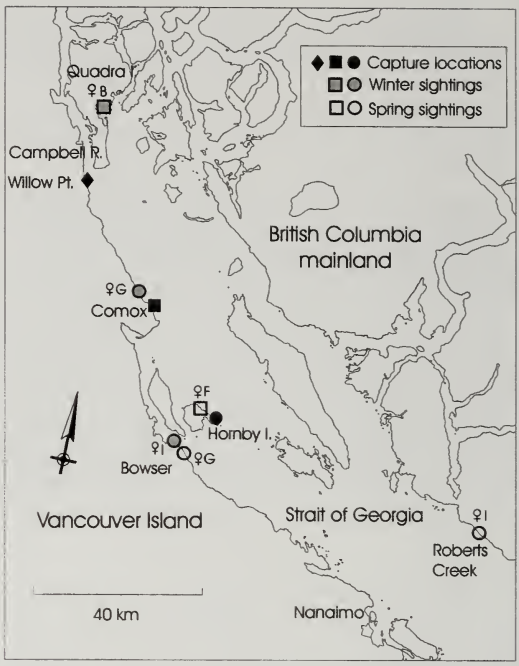

FIG. 1. Four of eight juvenile female Harlequin Ducks marked with external radio transmitters moved >10 km from their capture location in the northern Strait of Georgia, British Columbia, Canada, 2000–2001. Capture locations are shown as solid symbols; winter (mid-October through February) and spring (March) sighting locations of females that moved >10 km are shown as partially filled and unfilled symbols, respectively, with the type of symbol indicating the capture location from which the individual originated. Individual females are identified with letters (see also Table 2).

anchors; six weighed 3 g each with 1-cm wire anchors. We distributed radio types equally between the sexes. Radio transmitters weighed a maximum of 2% of body mass for all juveniles and were assumed not to affect behavior.

Researchers reported sightings of individuals marked with colored bands from 1995–2001 during the fall (August to October), when postjuvenile birds molt, and during spring (March), when many Harlequin Ducks aggregate at Pacific herring (*Clupea pallasi*) spawning sites (Rodway et al. 2003b). At these times birds spend less time feeding than during winter and frequently haul out on shoreline rocks. Two to several observers typically searched for marked birds for a number of days approximately equivalent to 1–6

weeks during fall, and 1–4 weeks during spring. From September to December 2000, I located juveniles with radio transmitters from land, or with fixed-wing aircraft. I conducted three telemetry flights in October and November and covered the northern Strait of Georgia, from the northern end of Quadra Island to Nanaimo (Fig. 1) at least once, and most areas at least twice. I determined distances individuals had moved from capture locations using a handheld GPS unit or from measurements taken from marine charts. I report records during winter (mid-October through February) separately from those during spring (March) because movement during spring can be associated with aggregation at herring spawning sites (Rodway et al. 2003b). I could not compare movement distances between radio-marked males and females due to small sample size of surviving males (see results). However, I was able to compare philopatry between the sexes by comparing proportions of all marked juveniles (captured before 2000) observed at their capture location during their second winter at the coast.

I was able to monitor survival of most juveniles carrying transmitters from September through November, until batteries failed or transmitters were lost, after which juveniles were resighted opportunistically. I confirmed the death of radio-marked juveniles by pinpointing their transmitters to small areas (several m^2) of dense shoreline vegetation (two cases), or by retrieving the carcass (one case).

I estimated local survival rates and tested hypotheses that they differed by sex and by age (juvenile and postjuvenile) using sightings of all juveniles marked with bands (21 females, 13 males) and the CMR program MARK (White and Burnham 1999). I developed a candidate model set that included the models containing effects necessary to test my hypotheses and that were based on *a priori* biological and sampling information (Lebreton et al. 1992, Anderson and Burnham 1999). Because sightings were recorded biannually (fall and spring), I estimated survival rates for 6-month periods, with the juvenile age class considered to last for one year (two 6-month periods). Biannual sightings permitted estimation of season specific survival and sighting rates, the inclusion of which I expected would improve model fit. Juveniles remain at the coast during their first summer and likely gain experience over time, suggesting that survival may be lower during winter (fall to spring) than summer (spring to fall); postjuvenile females incur costs of breeding during summer suggesting that their survival is likely higher during winter than summer (Robertson and Goudie 1999, Cooke et al. 2000). I also expected sighting rates to differ between fall and spring due to seasonal differences in observer effort and bird behavior. Models in the candidate model set therefore included those with and without the effects of age, sex, and season on survival, and with and without the effect of season on sighting rates (Table 1). I assumed that sighting probabilities did not differ by sex or age. Models with time dependence had too many parameters for the data to be fit properly. Competing models were ranked using Akaike's Information Criterion (AIC), which is based on the concept of statistical parsimony and is calculated as the best compromise between minimizing the number of parameters and maximizing model fit (Lebreton et al. 1992, Anderson and Burnham 1999, Cooch and White 2001).

I evaluated model fit and overdispersion with bootstrap goodness-of-fit testing (Cooch and White 2001). In this method, encounter histories are simulated using model parameters, generating simulated data sets that exactly meet model assumptions that individuals behave independently and that their rates are identical within classes (Lebreton et al. 1992). Comparison of observed and simulated model deviances then allows evaluation of model fit and estimation of the variance inflation factor, $\hat{c}$, a measure of the magnitude of overdispersion. I adjusted model fit for overdispersion and used the Quasi Akaike's Information Criterion (QAICc) to indicate models substantially supported by the data. I determined relative model support by the ratio of QAICc weights. Effects of band wear (Regehr and Rodway 2003) were unlikely to bias estimates of juvenile survival rates because bands wear little during their first year; however, band wear likely caused the survival rates of the postjuvenile age class to be underestimated slightly.

I used Fisher's exact test to compare proportions of juveniles dying to those remaining

TABLE 1. Candidate models ranked in order of increasing $QAIC_c$ indicate that survival rate differs by age (juvenile versus postjuvenile) and resighting rate differs by season (fall versus spring) for banded Harlequin Ducks, captured as juveniles, in the northern Strait of Georgia, British Columbia, 1995–2000. AIC_c values were adjusted for ĉ of 1.24.

Model description	Number of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
Survival rate differs by age, sighting rate differs by season	4	114.26	0.00	0.4552
Survival rate differs by sex, sighting rate differs by season	4	115.28	1.02	0.2728
Survival rate differs by age and sex, sighting rate differs by season	6	115.88	1.62	0.2020
Survival rate differs by age, sex, and season for the juvenile age class, sighting rate differs by season	8	119.21	4.95	0.0382
Survival rate differs by age, sex, and season for the juvenile age class and for postjuvenile females, sighting rate differs by season	9	120.17	5.91	0.0237
Survival rate differs by age, sex, and season for both age classes, sighting rate differs by season (general model)	10	122.32	8.06	0.0081
Survival and sighting rates are constant	2	138.56	24.30	0.0000
Survival rate differs by age, sighting rate is constant	3	139.65	25.39	0.0000
Survival rate differs by sex, sighting rate is constant	3	140.21	25.95	0.0000
Survival rate differs by sex and age, sighting rate is constant	5	142.07	27.81	0.0000

in their capture location. I set type I error rate at 0.05.

RESULTS

Among radio-marked juveniles, a greater proportion of males died (50%, $n = 6$) than did females (0%, $n = 9$; Fisher's exact test, $P = 0.044$). All deaths occurred within 46 days after capture. Two of the males that died were unusually light at capture (males N and O, Table 2). The death of the third male 46 days after capture (male K, Table 2) most likely was due to predation; four days earlier he had been observed 2 km from his capture location, feeding alongside two juvenile females. Based on sightings during and after the study period, I determined that ≥8 of the 9 radio-marked females survived the winter.

I contrasted 10 models in CMR analysis to test hypotheses that local survival rates differed by sex and age, and to estimate sex and age specific local survival rates (Table 1). Bootstrap goodness-of-fit testing with 1,000 simulations revealed adequate model fit; the probability of a deviance as great or greater than that of the most general model was 0.12, and the variance inflation factor, ĉ, was estimated at 1.24. Three models had similar QAICcs (differing by <2), thus they were fairly similar in their abilities to describe the data in a parsimonious manner and I drew inferences from this subset of models (Lebreton et al. 1992, Anderson and Burnham 1999). The most saturated of the three models estimated separate 6-month local survival rates for juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31–0.80), postjuvenile males (0.94 ± 0.09 SE; 95% CI = 0.44–1.00), juvenile females (0.84 ± 0.08 SE; 95% CI = 0.61–0.95), and postjuvenile females (0.89 ± 0.06 SE; 95% CI = 0.71–0.96). Based on these rates I built an additional model in which survival of juvenile males was set different from all other sex-age classes (four parameters). This model was well supported by the data (QAICc = 111.84, with 3.4 times the support of the highest ranking model in Table 1), indicating that local survival of juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31–0.81) was different from all other sex-age classes, and that I was unable to detect differences in local survival among juvenile females, postjuvenile females, and postjuvenile males (0.88 ± 0.04 SE; 95% CI = 0.77–0.94). Models were improved consistently by including the effect of season on sighting rates (fall: 0.31 ± 0.09 SE; 95% CI = 0.16–0.51; spring: 0.95 ± 0.05 SE; 95% CI = 0.72–0.99), but inclusion of season specific survival rates did not improve model fit.

Of the three potentially surviving radio-marked males (Table 2), one may have left the study area (male L). I last detected his radio

TABLE 2. Maximum movement distances from the capture sites of radio-marked juvenile female (f) and male (m) Harlequin Ducks during winter (mid-October through February) and during the herring spawning period in spring (March) in the northern Strait of Georgia, British Columbia, 2000–2001. At least 25% of females moved >30 km from their capture sites during winter and spring. Three of six radio-marked males died (marked with an asterisk). Locations are given in parentheses (see Fig. 1) for movement distances >10 km.

				Winter location			Spring location	
Identity code	Sex	Mass at capture (g)	Capture location[a]	Maximum movement distance (km)	Months recorded[b]	Number of records[c]	Maximum movement distance (km)	Number of records[c]
A	f	580	Comox	unknown[d]	—	—	unknown	—
B	f	570	Comox	48 (Quadra)	Oct.–Nov.	4	unknown[e]	—
C	f	515	Comox	3	Oct.–Feb.	9	4	4
D	f	500	Comox	7	Oct.–Jan.	7	3	1
E	f	485	Comox	3	Oct.–Feb.	8	1	1
F	f	610	Comox	2	Oct.–Feb.	7	35 (Hornby I.)	8
G	f	530	Hornby I.	36 (Comox)	Jan.–Feb.	3	11[f] (Bowser)	1
H	f	460	Hornby I.	1	Nov.–Jan.	3	4	4
I	f	535	Hornby I.	12 (Bowser)	Oct.	3	35 (Roberts Creek)	1
J	m	605	Willow Pt.	unknown[g]	—	—	unknown	—
K*	m	590	Comox	2	Oct.	1	—	—
L	m	565	Comox	15[h]	Nov.	1	unknown	—
M	m	485	Hornby I.	unknown	—	—	2	6
N*	m	415	Hornby I.	—	—	—	—	—
O*	m	410	Hornby I.	—	—	—	—	—

[a] Juveniles were captured 3–14 September 2000.
[b] Range of months during which records were obtained for winter location.
[c] Number of sightings and detections of radio frequency at winter or spring location, with maximum of 1/day.
[d] Radio lost 7 km from capture location on tidal shelf; individual sighted during spring 2002.
[e] Winter location could not be surveyed during spring.
[f] Also seen once at Hornby Island, 2 km from capture location.
[g] Located four days following capture, then probably lost radio.
[h] Radio signal last indicated a location about 15 km south of capture site on 11 Nov.

signal about 15 km south of his capture site, possibly over open water, 64 days after capture. Although I conducted a telemetry flight over the entire study area six days later, he was never found again. I could not locate the second male (male M) during winter but sighted him close to his capture location on Hornby Island during March, suggesting a lost or malfunctioning radio during winter. The third male (male J) was observed 10 km north of his Campbell River capture location four days after capture but was never sighted again. This male received a 3-g transmitter with a small subcutaneous anchor which he probably lost shortly after this sighting.

Of nine radio-marked females, I was able to determine the locations of eight during winter, and of seven during both winter and spring (Table 2, Fig. 1). I could not relocate one female (female A) because she lost her radio 7 km from her capture site soon after capture; she was confirmed alive during spring 2002. Female B was not resighted during spring; however, her wintering location at Quadra Island could not be revisited at that time. The mean maximum distances females were found from their capture locations were 14.0 km ± 6.3 SE (n = 8) and 13.2 km ± 5.7 SE (n = 7) during winter and spring, respectively.

I detected no significant difference between the sexes in the proportion of marked juveniles resighted at their capture location during their second winter (males: 29%, n = 7; females: 25%, n = 12; Fisher's exact test, $P > 0.99$).

DISCUSSION

Results of this study provide new information important to understanding the postfledging ecology and population dynamics of Harlequin Ducks. First, radio marking of juvenile females indicated that, contrary to previous evidence for philopatry (Robertson and Goudie 1999, Cooke et al. 2000), some juvenile females moved substantial distances during winter. Second, contrary to predictions from theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and An-

derson 1988, Anderson et al. 1992), and assumptions of male-biased dispersal in young Harlequin Ducks (Cooke et al. 2000), proportions of banded male and female juveniles resighted at their capture locations during their second winter did not differ, suggesting equal dispersal rates. Third, radio marking in combination with CMR analysis indicated that first-winter survival of juvenile Harlequin Duck females was high, providing further evidence that female winter survival may be similar among age groups. Conclusions pertaining to female survival rates must, however, be treated with caution due to sample size limitations.

Results of this study also suggest that juvenile male Harlequin Ducks may be more likely to die than juvenile females. However, inferences regarding differences in survival between the sexes are weak due to small sample sizes of radio-marked birds. Although lower survival of juvenile males relative to the other sex-age classes also was supported by CMR analyses, the local survival rates estimated by CMR analysis reflect a combination of mortality and emigration, and large confidence intervals surrounding point estimates limit confidence in apparent differences. The reason for a higher death rate of male than female juveniles is not clear, but might be related to differences in vulnerability to predation resulting from differences in conspicuousness of plumage, or to differences in susceptibility to the effects of food shortage due to larger size and higher growth rate of males (Clutton-Brock 1986, Cooch et al. 1997). My results suggest that the assumption that low local survival of juvenile and subadult males reflects emigration and not mortality (Cooke et al. 2000) should be re-assessed.

Juvenile survival rates generally are lower than those of adults in waterfowl (Johnson et al. 1992). However, most juvenile mortality occurs during the prefledging and migration periods (Nichols and Hines 1987, Francis et al. 1992, Johnson et al. 1992), and hunting mortality tends to be juvenile biased (Bellrose 1980). The high winter survival observed for juvenile Harlequin Duck females in this study therefore may at least partly reflect the fact that juveniles were captured after migrating to wintering areas and that hunting mortality is low for Harlequin Ducks on the western coast of North America (Robertson and Goudie 1999). Results of this study, in combination with that of Cooke et al. (2000), who primarily included subadult (second and third year) and adult (after third year) females in CMR analyses, suggest little difference in winter survival rates of female Harlequin Ducks of different ages, provided that juveniles have completed their first migration, and that these rates likely can be set equal for estimates of recruitment into the breeding population. However, the possibility remains that the similar adult and subadult female local survival rates observed by Cooke et al. (2000) were due to subadults having lower death rates balanced by higher emigration rates (Cooke et al. 2000). Also, conclusions pertaining to juvenile females remain tentative due to sample size limitations in this study. Clearly, size of the study area also may affect conclusions. Considering movement rates and distances observed in this study, reduced juvenile female local survival due to emigration would be more likely if the study area were small. Summer survival rates of juvenile and subadult females might be expected to be somewhat higher than those of adult females because at least some immature females do not breed and hence do not incur associated mortality (Robertson and Goudie 1999, Cooke et al. 2000).

Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and ≥25% of radio-marked females moved >30 km from their capture location. These results were unexpected, based on previous evidence for juvenile female philopatry (Robertson and Goudie 1999, Cooke et al. 2000), and theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992). However, I was unable to compare movement distances between sexes. Dispersing juvenile male Harlequin Ducks may move greater distances than dispersing juvenile females, as has been observed for some other waterfowl species (Kirby 1976, Rienecker 1987, Baldassarre et al. 1988). One of three surviving radio-marked males may have left the study area, whereas no female did. Individuals that disperse greater distances are less likely to be resighted than those moving smaller distances. Thus, greater

male dispersal distances, possibly in combination with higher death rates, could account for lower local survival of male than female juveniles.

Results of this study have implications for genetic and demographic population structure of Harlequin Ducks. Juvenile Harlequin Ducks are believed to leave inland breeding areas and arrive at coastal wintering areas in family groups accompanied by their mothers, at least when families are intact at the time of fledging (Regehr et al. 2001). In this study, juveniles of both sexes dispersed from their coastal capture locations, suggesting that both sexes likely contribute to gene flow among populations. Also, dispersal of females in addition to males increases the potential for demographic connection among populations because successful recolonization or rescue of extinct or reduced populations are dependent upon female movement (Avise 1995). Further study is required to test the idea that low local survival rates of juvenile males may be partly due to higher death rates, to resolve potential sex differences in juvenile dispersal distances, and to investigate what factors affect differences in dispersal strategies among individuals of the same sex. Exceptions to patterns of sex-bias in subsets of populations can aid in our overall understanding of the evolutionary forces shaping dispersal patterns.

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POPULATION RECOVERY OF THE EASTERN BROWN PELICAN FOLLOWING ITS EXTIRPATION IN LOUISIANA

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ABSTRACT.—We report on the exponential growth of the Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) in Louisiana, following its extirpation in 1963, and its subsequent reintroduction (1968–1980). This population growth pattern is remarkable since the Brown Pelican exhibits low fecundity, a long life span, and is considered largely nonmigratory in the Gulf of Mexico. To understand the regional changes in breeding numbers of Brown Pelicans in the northern Gulf of Mexico, we investigated the long term trends of the other subpopulations in Florida and Texas. The Florida subpopulation of Brown Pelicans has exhibited a stable-limit cycle, but within the last decade the number of nesting birds has declined while the number of nesting colonies has steadily increased. The number of Brown Pelicans in Texas now exceeds estimates prior to the time pesticides caused reproductive failure of the subpopulation. The Louisiana subpopulation now equals or exceeds its historical (pre-pesticide) numbers. Although local recruitment can account for the exponential growth of Brown Pelicans in Louisiana, we believe that dispersal from colonies outside of Louisiana may have augmented the growth of its nesting population. *Received 11 February 2003, accepted 15 October 2003.*

Prior to the 1930s, estimates of the Louisiana subpopulation of the Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) ranged from 12,000–85,000 (Lowery 1955, 1974; King et al. 1977; Wilkinson et al. 1994), with a conservative estimate of 50,000 individuals for Texas and Louisiana combined (Schreiber 1980). Extirpation of the Brown Pelican in Louisiana had occurred by 1963 (Williams and Martin 1968), and the last recorded nesting effort of the native population was observed in 1961 (Van Tets 1965). During this same period, a severe decline in the Texas subpopulation occurred, and King et al. (1977) estimated that by 1961 <50 adults remained in Texas. Despite the extreme losses in Texas and Louisiana, the number of Brown Pelicans nesting in Florida remained generally stable (Williams and Martin 1968, Kushlan and Frohring 1985, Wilkinson et al. 1994).

While reproductive failure from organochloride pesticide contamination caused the decline of pelicans in Texas (King et al. 1977, 1985), the extirpation of Louisiana's subpopulation was attributed to direct bird mortality (Blus and Joanen 1975) and more recently to a reduction in prey abundance resulting from endrin contamination (Biglane and LaFleur 1967; Colten 2000, 2001). The rapid disappearance of the Brown Pelican (Norman and Purrington 1970) coincided with endrin use and production discharges (1958–1964) and massive fish kills (1963–1964) caused by endrin contamination (Mount and Putnicki 1966). However, it was not until 1975, when a severe die-off of pelicans (after reintroduction) in Louisiana occurred, that the extreme sensitivity of pelicans to endrin contamination was documented (Blus et al. 1979).

In 1968, the Louisiana Dept. of Wildlife and Fisheries and the Florida Fish and Wildlife Conservation Commission began reintroduction of the Brown Pelican into coastal Louisiana. A total of 1,276 Florida nestlings were transplanted from six colonies in Florida to three sites in Louisiana between 1968 and 1980 (for detailed transplanting information see Nesbitt et al. 1978, McNease et al. 1984). The first nesting attempts of transplanted birds occurred during the spring of 1971, and at that time, the birds were almost 3 years old (Williams and Joanen 1974). During the spring of 1975, endrin pollution caused a die-off of about 40% of a standing population of 400–450 Brown Pelicans (Winn 1975, Nesbitt et al. 1978, Blus et al. 1979). Since then, the Louisiana population has continued to grow.

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The objective of our study was to investigate the long term growth trend of the Eastern Brown Pelican in the Gulf of Mexico, with an emphasis on the nesting birds in Louisiana, and compare these numbers to those of Florida and Texas. Given that the Louisiana subpopulation has exhibited an exponential increase of nesting birds, we investigated the potential for local recruitment versus long distance emigration and dispersal from surrounding subpopulations in augmenting Louisiana's population growth.

METHODS

We used breeding Brown Pelican census data from Louisiana, Texas, and Florida, the states comprising the largest subpopulations of breeding pelicans along the U.S. Gulf of Mexico. These data were based on nest counts (Florida and Louisiana) or breeding pairs (Texas); hereafter, nest numbers are used as a common unit of measure. In Louisiana, pelican nests and nestlings were counted yearly (except 1991) with a mean of four flights (rotor or fixed-wing) per year (1993–2001). The nesting data were collected by the Louisiana Dept. of Wildlife and Fisheries (Hess and Linscombe 2001). Surveys prior to 1993 usually involved a combination of aerial and ground census techniques, as summarized by McNease et al. 1992. In Texas, breeding pairs were estimated as described in the Texas Colonial Bird Survey (Lange 1993). Nesting pair data from Texas were provided by the U.S. Fish and Wildlife Service (Houston, Texas). The Florida Fish and Wildlife Conservation Commission collected Florida nesting data. Nest counts in Florida were conducted during peak nesting periods and summarized between two zones: Atlantic and Gulf of Mexico coasts.

We used an exponential growth equation ($N_t = N_o e^{rt}$) to calculate the intrinsic growth rates of nesting subpopulations in Louisiana and Texas (Manugistics, Inc. 1995). In the equation above, N_t is the estimated number of nests for a given year, N_o is the initial number of nests at time zero, r is the intrinsic growth rate, and t is the time in years. Number of nests and time served as dependent and independent variables, respectively.

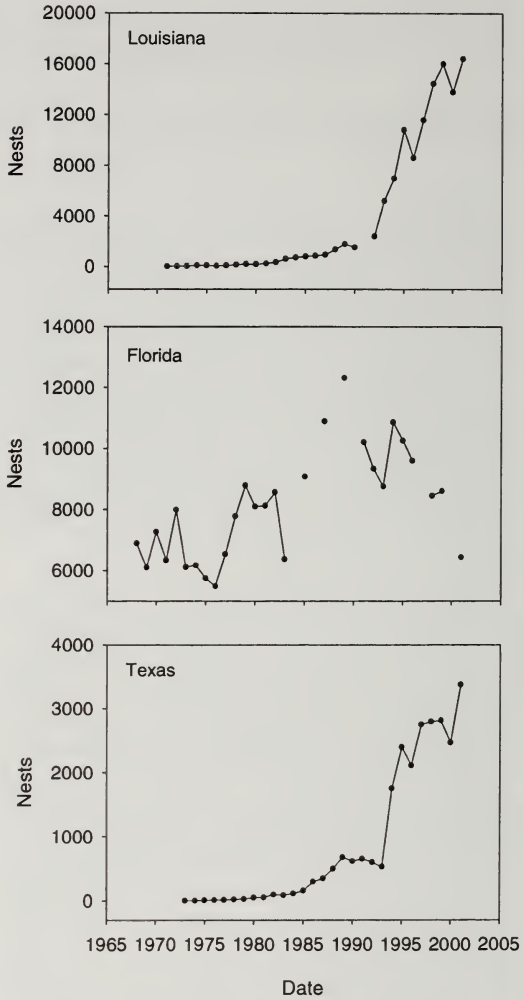

FIG. 1. The Brown Pelican breeding populations in Louisiana and Texas have grown exponentially while declines occurred in Florida.

RESULTS

Louisiana.—The population of nesting pelicans in Louisiana has grown exponentially from 1971–1999, with slower rates of growth occurring during 1999–2001 (Fig. 1). During 2001, the population peaked at 16,405 nests (Fig. 1). A best-fit exponential model describing population growth from 1971–2001 suggested an intrinsic growth rate (r) = 0.25 (R^2 = 0.97).

The overall (1971–2001) mean nestling production per active nest was 1.66. Peak nestling production occurred in 2001 with 34,641 young produced; at this time the high-

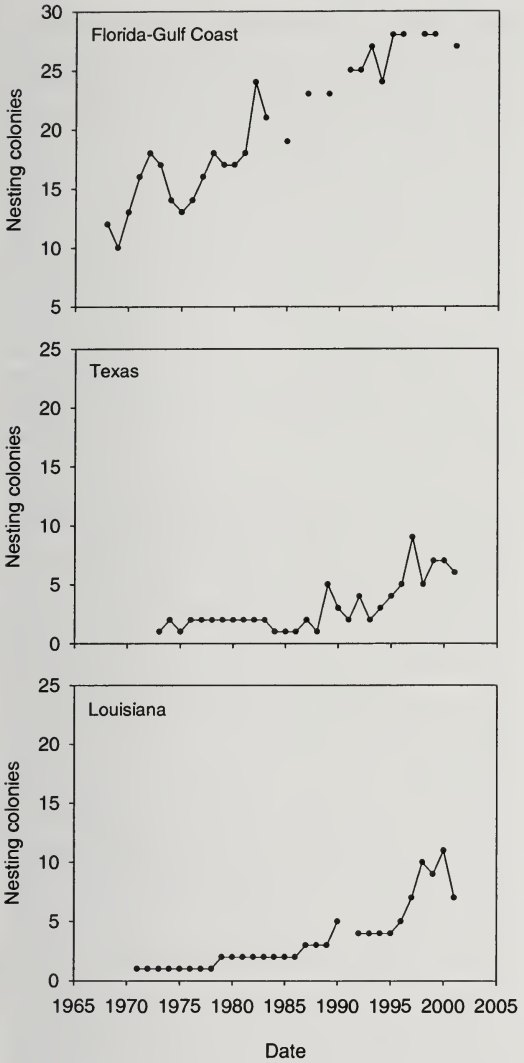

FIG. 2. While the number of Brown Pelican colonies increased along Florida's Gulf coast (a mean of one colony every two years since 1968), the number of nesting birds decreased (see Fig. 1). The number of nesting colonies in Texas and Louisiana has remained low despite the immense increase in the number of nesting birds.

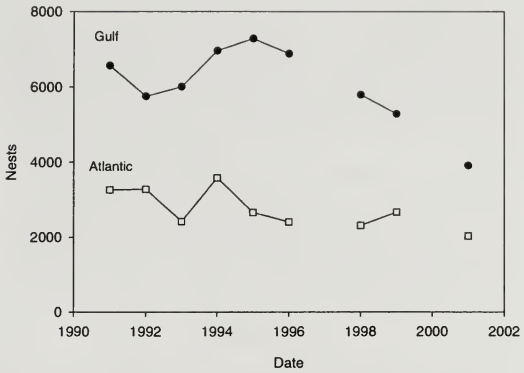

FIG. 3. In Florida, the Atlantic Brown Pelican subpopulation remained relatively stable from 1990–2001, but there was a decrease in the Gulf coast subpopulation.

est yearly mean number of nestlings per active nest (2.11) was recorded for Louisiana. The peak number of nesting colonies (11) in Louisiana occurred during the 2000 breeding season (Fig. 2). An interannual increase in nest production (2,639) occurred from 2000–2001; concomitantly, four nesting colonies were abandoned (Fig. 1, Fig. 2). In 2000, a new colony of approximately 10,000 nests was initiated on a 12-ha dredge spoil island (Baptiste Collette or Plover Island, near the mouth of the Mississippi River). This immense, concentrated shift comprised more than one-half of the total nesting population in Louisiana.

Interannual fluctuations in the Louisiana subpopulation occurred during the following three time intervals: 1989–1990, 1995–1996, and 1999–2000 (Fig. 1). Decreases in nest numbers during the spring of 1990 and 1996 correspond to years that had protracted freezing temperatures during the preceding winters. During 1999 and 2000, a 50–100 year local drought coinciding with low Mississippi River stages resulted in high estuarine salinity across the Louisiana coast.

Florida.—Florida nesting birds have exhibited cyclic changes in nest numbers from 1968 onward (Fig. 1). Following a general pattern of increasing growth from 1968–1990, statewide pelican nest numbers have declined over the past decade, and the number of nests (6,432) in 2001 fell below the 1968–1990 mean of approximately 8,000 nests.

The decline in the number of nests in Florida has occurred most noticeably among the Gulf coast colonies, while colonies located along the Atlantic coast have remained relatively stable (Fig. 3). Concomitant with the decline in nest numbers on Florida's Gulf coast, there was a linear increase in the number of colonies, and a mean (1968–2001) increase of one colony every two years (Fig. 2).

Texas.—A peak nesting population of 3,373 breeding pairs among a total of seven colonies

was recorded for Texas in 2001 (Fig. 1). The mean number of nesting pairs from 1997–2000 was 2,839. The Texas population has grown exponentially with an intrinsic growth rate (r) = 0.22 (R^2 = 0.94, Fig. 1). Fluctuations in the number of nesting pairs in Texas are similar to those observed in Louisiana with noticeable interannual peaks and declines occurring during 1989–1990, 1995–1996, and 1999–2000 (Fig. 1).

DISCUSSION

Since its extirpation and reintroduction, the Eastern Brown Pelican in Louisiana has provided a remarkable example of exponential growth of a nonmigratory population (Palmer 1962) of long-lived (>20 years) birds. Newly introduced species, with rapid maturation and high annual fecundity, commonly exhibit exponential population growth. For example, Bock and Lepthien (1976a, 1976b) found that populations of Cattle Egrets (*Bubulcus ibis*; r = 0.21, 1956–1971) and House Finches (*Carpodacus mexicanus*, r = 0.23, 1962–1971) grew exponentially after their introductions into regions of the United States. Interestingly, the Louisiana pelican subpopulation has grown at intrinsic rates similar to that of "r-selected" bird species. This raises the question of whether local recruitment can account for the rapid increase in the Brown Pelican nesting population in Louisiana.

Based on a simple exponential model, local recruitment could explain the observed growth of the Brown Pelican population in Louisiana, provided that the estimated growth rate is 0.25/year. However, since this rate is as high as those observed in r-selected species, we suggest an alternative explanation, i.e., that immigration into Louisiana has augmented this growth. This immigration may have involved subadult pelicans, produced elsewhere, joining the Louisiana nesting population. This hypothesis also would explain the protracted decline in the Florida Gulf coast population concurrent with the rapid increase in the Louisiana breeding population.

The ability to detect emigration into Louisiana from banded birds has been constrained by the remoteness of pelican breeding and feeding areas in Louisiana. However, the steady increase of nesting colonies on Florida's Gulf coast, while nest numbers decreased, does indicate that pelicans in Florida are seeking either new nesting habitat or improved forage conditions, or they are avoiding disturbance. Schreiber (1976) believed that food availability was the main reason for movement of nonbreeding Brown Pelicans. Adjacent to Florida, Alabama's Gaillard Island nesting colony has grown rapidly; there were four nests in 1983 (the first account of nesting pelicans recorded in the state), and the population peaked in 1999 with approximately 5,200 nests (R. B. Clay pers. comm.). From early band returns, Wood et al. (1995) concluded that the Alabama colony (Gaillard Island) was initiated by birds from the panhandle of Florida.

Dispersal from natal colonies.—In a long term analysis of Brown Pelican band returns, Schreiber and Mock (1988) concluded that Florida's west coast (Gulf of Mexico) birds comprised a distinct subpopulation from that of Louisiana's. In their study, 82% of band returns were from Florida's Gulf coast, indicating a largely resident population. Other band returns were from the Keys (8%), Cuba (5%), and Alabama (1%), but none were reported from Louisiana. In a later study on pelican dispersal, Wood et al. (1995) found, conversely, that banded birds from a natal colony on the Florida panhandle moved both eastward and westward along the Gulf coast, and movement into Louisiana was documented (though only one band was recovered in Louisiana).

Long range dispersal of pelicans throughout the Gulf of Mexico has been reported historically (Mason 1945, Schreiber and Mock 1988, Sykes and Langridge 1991, Johnsgard 1993, Wood et al. 1995). As of 2001, banded pelicans from Louisiana have been reported from every Gulf coast state, and also from Cuba, the Yucatan Peninsula, Belize, and Guatemala (J. Harris pers. comm.). These recent Louisiana band returns confirm earlier findings (Mason 1945, Schreiber 1976) that Brown Pelicans, especially juveniles, move randomly and for long distances. A distinct pattern of dispersal from Louisiana's colonies, however, is not discernable at this time.

Whether breeding birds are shifting toward the northernmost portions of the Gulf of Mexico remains debatable. Nonetheless, this pattern is conceivable given the northward ex-

pansion of breeding colonies along the Atlantic coast of the U.S. Since 1980, first breeding records for Brown Pelicans have been reported for Georgia, Virginia, Maryland, Delaware, and New Jersey (see Wilkinson et al. 1994). Warm temperatures may facilitate a northward dispersal pattern, and the warmest decade since instrumentation began (1861) occurred 1990–2000 (Houghton et al. 2001). An interdecadal comparison between the 1980s and mid-1990s showed a notable reduction in pelican numbers (>70% or 1,300 individuals) in Puerto Rico and the U.S. Virgin Islands (Collazo et al. 1998). The authors did not find evidence of reproductive failure or nesting and roosting habitat changes.

Limitations on population growth.—Nelson (1979) proposed that populations of pelaniform species are controlled mostly by environmental factors (climate and food availability). Fledging success of the California subspecies (*P. o. californicus*) was dependent on the local abundance of northern anchovy (*Engraulis* sp.; Anderson et al. 1982). Along the Pacific coastlines of North and South America the importance of food abundance on seabird mortality is well understood, especially as it is related to El Nino-Southern Oscillation events (Duffy et al. 1988). In the Gulf of Mexico, relationships between food supply and breeding success have not been widely studied. Poor food availability, however, has been implicated in reproductive failures in southern Florida near the Keys (Kushlan and Frohring 1985). Moreover, there was a strong, positive association between statewide mullet (*Mugil* spp.) landings and Brown Pelican nesting effort in Florida during the period 1968–1992 (Nesbitt et al. 1996). Whether food supply has influenced decreasing nest numbers along Florida's Gulf coast is unknown.

Other density independent forces such as human disturbance (Jehl 1973, Anderson and Keith 1980, Anderson 1988) inhibit successful breeding at local levels and may influence colony site selection or abandonment. There are significant differences, for example, in human population growth in the coastal areas among Louisiana, Florida, and Texas (Barrett 2001). From 1990 to 2000, the human population on Florida's Gulf coast has increased 20.8%, and Texas' population has grown 18.7%. In contrast, the population of coastal parishes in Louisiana has grown only 4.8%. Thus, habitat fragmentation by coastal land development and the probability of nesting colony disturbance is of greater concern in Florida and Texas than in Louisiana.

Habitat stability.—The greatest future problem for Brown Pelicans in Louisiana is the stability of natural nesting habitat. Barrier islands in Louisiana are the aging relics of Mississippi River deltas, and the rapid erosion of these islands has been largely irreversible, as there is little "new" sand or coarse-grained material entering the system. This has resulted in the need to replenish, with dredge material, historically successful natural nesting islands in Louisiana. The use of created islands (dredge material) by nesting pelicans has been encouraging in Louisiana and elsewhere (Wood et al. 1995). High rates of island fragmentation in Louisiana conceivably could facilitate the establishment of new colonies that have reduced predator activity (Kushlan and Frohring 1985). The fact that within one year more than 60% of the nesting population initiated a colony on a relatively small dredge spoil island reflects this species plasticity to changes in habitat.

The mean number of nests per colony in Louisiana in 2001 (2,344 nests per colony) is an order of magnitude higher than that of Florida's statewide density (161 nests per colony). The exponential increase in nests we observed in Louisiana contrasted with the disproportionate number of new nesting colonies suggests that a sustained amount of nesting habitat, rather than food availability, will be a future concern in Louisiana. In Florida, the decrease in the number of nesting pairs along the Gulf coast, with no decline in the number of colonies, is the reverse of what is being seen in Louisiana. In Florida, the food base, rather than the availability of suitable nesting sites, may limit the population.

In general, the growth of the subpopulations of Brown Pelicans in Louisiana, Texas, and Alabama, during periods when declines were observed along the Gulf coast of Florida and Puerto Rico and in the Virgin Islands, indirectly suggests that Brown Pelicans may have the ability to shift to habitats where suitable nesting and forage conditions exist outside of intense human disturbance.

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SEASONAL VARIATION IN AVIAN COMMUNITY COMPOSITION IN A HIGH-ANDEAN *POLYLEPIS* (ROSACEAE) FOREST FRAGMENT

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ABSTRACT.—We analyzed seasonal variation in avian species richness and relative abundance at the community and guild level during a 13-month period in central Bolivia in an 11-ha patch of *Polylepis* (Rosaceae) forest, a high-Andean ecosystem that has suffered from extreme anthropogenic fragmentation. Birds were surveyed audio-visually (supplemented with mist net data) and assigned to five relative abundance categories for 2-month survey periods. We recorded 35 core species, including 16 insectivores (46%), 11 frugi-granivores (31%), seven nectarivores (20%), and one carnivore (3%). Core species richness varied from 25 (June–July) to 33 (October–November). Insectivores had a significantly higher proportion of year-round residents (81%) than frugi-granivores (45%) or nectarivores (14%); the same trend was evident with respect to seasonal variation in species richness of each guild. Although most species varied considerably in their relative abundance, no guild showed significant variation in relative abundance scores among survey periods. However, frugi-granivores and nectarivores combined, both of which depend upon plants as food resources, reached a significant minimum in mid-winter (June–July), and the same result was found at the community level. The insectivore guild thus was the most temporally stable both in terms of species richness and abundance. Qualitative observations indicated that the fluctuations in frugi-granivores and nectarivores were related to the availability of food resources. *Received 22 April 2003, accepted 1 August 2003.*

Seasonal variation in the composition of Neotropical bird communities has been investigated in only a small number of case studies (Karr 1976, Brooks 1997, Hilty 1997, Schmitt et al. 1997). Such research often is hampered by high levels of Neotropical community diversity, a fairly large proportion of hard-to-detect cryptic or naturally rare species, and logistic constraints. These factors frequently impede the use of standard survey techniques and make it difficult to obtain sufficiently complete, comparable species inventories (Herzog et al. 2002a). Most studies on seasonal variation therefore have limited their scope to subsets of communities, such as hummingbirds (Stiles 1980, 1985a), understory frugivores (Loiselle and Blake 1991), mixed species flocks (Develey and Peres 2000), or canopy birds (Loiselle 1988).

Temporal variability in community structure is caused by local movements (Karr and Freemark 1983, Fjeldså 1991, Davis 1993), altitudinal migration (Stiles 1988, Loiselle and Blake 1991), or long distance latitudinal migration (e.g., Marantz and Remsen 1991, Davis 1993) of a considerable number of species. Movement and migration patterns have been hypothesized or documented to reflect food resource availability (Karr 1976, Stiles 1980, Loiselle 1988, Blake and Loiselle 1991, Loiselle and Blake 1991, Levey and Stiles 1992, Brooks 1997). Different food resources tend to show asynchronous abundance peaks (Karr 1976, Develey and Peres 2000), and different guilds therefore may be expected to show dissimilar patterns, but little data for within-community comparisons are available to test this prediction (but see Blake and Loiselle 1991).

Based on studies in lowland Panama, Karr (1976) hypothesized that in the tropics seasonal variability in diversity should increase from omnivores to frugivores to insectivores. This was supported by Brooks (1997), who found the highest seasonality for insectivores in the Paraguayan *chaco*. In Neotropical montane forests, however, most altitudinal migrants, which often comprise >30% of local avifaunas (Loiselle and Blake 1991), are frugivores or nectarivores (Stiles 1985b, Blake et

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al. 1990, Hilty 1997), and insectivore fluctuations therefore may have little impact on community composition in this habitat. Thus, studies in other habitats and biogeographic regions are required to determine general patterns and key factors determining the composition of tropical bird communities.

We analyzed seasonal variation in species richness and relative abundance at the community and guild level in a high-Andean *Polylepis* (Rosaceae) forest fragment during a 13-month period in central Bolivia. Specifically, we investigated whether seasonal changes in community richness and overall abundance occurred, and if insectivores showed more pronounced seasonality than other guilds in this marginally tropical, high-elevation forest ecosystem as proposed by Karr (1976) for the tropical lowlands. Since *Polylepis* forests have suffered from strong anthropogenic fragmentation (Fjeldså and Kessler 1996, Kessler 2002), we paid particular attention to abundance patterns of habitat specialists to assess implications for their conservation.

STUDY AREA AND METHODS

Study area.—We studied the bird community of an 11-ha fragment of *Polylepis besseri* forest located just north of the small community of Sacha Loma in the department of Cochabamba, Bolivia (17° 44′ S, 65° 34′ W, 3,710–3,880 m elevation) from November 1999 to November 2000. The fragment consisted of 9.3 ha of forest enclosing a 1.7-ha boulder field largely devoid of vegetation. Tree height varied from 4–10 m. Shrubs (*Gynoxis*, *Berberis*, *Ribes*, *Baccharis*, *Brachyotum*) were distributed patchily, and the ground largely was covered by bunch grass (*Festuca*, *Stipa*, *Calamagrostis*). Except for some densely vegetated spots, most of the vegetation was open enough to allow unobstructed passage on foot. Human impact on the forest (cattle grazing, fire wood cutting) was low, but the surrounding grassland was used intensively for sheep grazing. For a detailed description of the vegetation see Fernández et al. (2001).

The study site is embedded in a landscape mosaic of high-Andean *puna* grassland and more or less isolated *Polylepis besseri* fragments (varying in size from 0.01–100 ha) in the transition zone from humid montane forests on the eastern Andean slope to dry intermontane valleys of southern Bolivia. The study fragment is 10 m from an about 40-ha forest patch with a considerably lower tree density and about 600 m from a 100-ha fragment with a similar vegetation structure. Climatic differences between seasons in the study area are pronounced. The rainy season (austral summer) extends from November to March, whereas dry conditions prevail from May to September during the austral winter. Brief transition periods occur in April and October. No climatic data are available for the study area, but Fernández et al. (2001) present temperature and precipitation values from two nearby climatic stations (Alalay, Toralapa) at elevations similar to that of the study fragment, however without stating the number of years of data. Mean annual precipitation at Alalay is 72 cm with a maximum of 17 cm in January. The five rainy season months combined receive over 60 cm of precipitation, whereas the five dry season months combined receive slightly less than 5 cm. Mean annual temperature at Toralapa is 8.7°C with monthly maxima of about 10–11° C in the rainy season, which drop to a minimum of about 7° C in June. Mean monthly minima drop to below freezing from April to October (with a minimum of about −5° C in June and July) and remain slightly above 0°C during the rainy season.

Field surveys.—We surveyed the *Polylepis* bird community for several days each month except in February and March 2000, when social unrest did not allow field work in Sacha Loma. Survey dates were 10–12 November and 7–12 December 1999, 27–31 January, 13–18 April, 10–13 and 24–29 May, 11–13 June, 2–4 and 9–11 July, 3–7 August, 15–17 September, 14–16 and 22–24 October, and 13–17 November 2000. SKH and RSA determined the presence and relative abundance of bird species by daily walks through the fragment during most of the daylight period, and we monitored vocal activity of nocturnal species from our camp site near the forest edge. We identified birds both visually and acoustically, and SKH was familiar with sight and sound identification of all species before beginning data collection. Also, we operated 10–15 mist nets daily during the same visits starting in

December 1999 (see Herzog et al. 2002b). We used intensive observations of foraging behavior (e.g., mixed species foraging flocks; Herzog et al. 2002b) and opportunistic examination of fecal material (mainly during handling of netted birds, rarely upon encounter in the forest; fecal matter was screened for presence of fruit pulp, seed remnants, or chitinous insect parts) to determine the primary diet of each species in the study area. For some species we also consulted standard references (e.g., Fjeldså and Krabbe 1990).

As some species and many individuals remained unmarked even after several months of banding operations, and because thorough spot map surveys of all species were unfeasible due to time constraints, we estimated relative rather than absolute abundances of species for each month based on the frequency of encounter of a given species. We distinguished five relative abundance categories: (a) rare, no more than three observations of single individuals or one observation each of a pair and a single bird, suggesting that no more than two to three individuals may have been present; (b) uncommon, single individuals or pairs observed occasionally but not daily, probably four to six individuals present; (c) fairly common, small numbers observed daily or almost daily, probably 7–12 individuals present; (d) common, observed repeatedly every day, probably 13–20 individuals present; and (e) abundant, observed daily in large numbers, >20 individuals present. Due to the biases of mist net capture data (e.g., Remsen and Good 1996), relative abundance estimates were based almost exclusively on visual and acoustical observations. For rare and uncommon species, we consulted data from mist net captures, and in a few cases we increased a species' relative abundance by one rank when mist net data indicated a slightly higher abundance than observational data.

Data analysis.—We included only core species (those that regularly breed, winter, or migrate through a given habitat; Remsen 1994) of the *Polylepis* fragment in the present analysis. Species considered rare visitors from nearby habitats, dispersing individuals, or vagrants were not analyzed. Valid, meaningful comparisons of community composition within or between sites require similar levels of sampling effort and survey completeness (Remsen 1994). Because survey effort varied among months, we combined monthly data into five 2-month periods based on climatic and biological characteristics: December–January (11 survey days), April–May (16), June–July (9), August–September (8), and October–November (14). December and January are the two months of greatest precipitation (Fernández et al. 2001) and correspond to the late breeding season for most *Polylepis* species (authors pers. obs.). April and May represent the transition period from the rainy to the dry season, whereas June and July are characterized by the lowest temperature and precipitation values (Fernández et al. 2001). The onset of territorial behavior in several core species occurs in August and September (Herzog et al. 2002b), followed by the peak of the breeding season for most *Polylepis* species (see Fjeldså and Krabbe 1990; authors pers. obs.) and the transition period from the dry to the rainy season in October and November.

Taking into account the small size of the forest fragment, its open vegetation structure, and relatively low species richness, as well as SKH's familiarity with the avifauna, we consider that despite the differences in survey effort >95% of all core species were recorded in each 2-month period (see also Fjeldså 1993 for an assessment of minimum survey effort in *Polylepis* woodlands). Although the April–May period received the highest survey effort, six days of field work during late May added only a single core species that had not been recorded during April or early May. This indicates that our assumption of >95% completeness in all periods is warranted.

We assigned all core species to one of four primary diet categories: insectivores (species that primarily consume insects and other arthropods), frugi-granivores (species that primarily consume fruit, seeds, and flowers), nectarivores (species that primarily consume nectar), and carnivores (species that primarily consume vertebrate prey). We ranked relative abundance categories on an ordinal scale of increasing abundance from 0 (not recorded) to 5 (abundant). If a species' abundance varied between months within the same 2-month period, the mean was used (e.g., 2.5 for a species uncommon in June and fairly common in July). However, a species that was rare in one month and not recorded in the other month of

a given 2-month period was still considered rare and assigned an abundance rank of 1.

We performed sign tests to analyze changes in relative abundance within guilds and for the entire bird community between consecutive 2-month periods using STATISTICA for Windows (StatSoft, Inc. 1997). We examined differences among guilds in the proportion of year-round residents with a Fisher exact test using StatXact (Cytel Software Corp. 1995).

RESULTS

Species richness.—We recorded a total of 35 core species, including 16 insectivores (46%), 11 frugi-granivores (31%), 7 nectarivores (20%), and 1 carnivore (3%; Table 1). An additional 25 vagrant or visiting species were observed in the study site (Appendix). Nineteen (54%) core species were year-round residents (i.e., they were recorded during all 2-month periods), whereas three core species (9%) each were observed during only one period. Among insectivores, 13 species (81%) were year-round residents, whereas only 5 frugi-granivores (45%) and 1 nectarivore (14%) were recorded during all periods. These differences in the proportion of year-round residents among guilds were significant (Fisher exact test, $P = 0.008$). The single carnivore, the Yungas Pygmy-Owl (*Glaucidium bolivianum*), was observed during all periods except December–January, but it may have been overlooked then due to its crepuscular and nocturnal activity.

Core species richness of the *Polylepis* bird community was lowest in winter, with 25 species during June–July and 26 species during August–September, and it was highest during the two transition periods, with 29 species during April–May and 33 species during October–November (Fig. 1A). The latter two months correspond to the height of the breeding season of most *Polylepis* birds (authors pers. obs.; see Fjeldså and Krabbe 1990). During December–January, species richness was slightly higher (27 species) than during winter. Insectivore richness showed low variability among periods, varying from 13 species during December–January to 16 species during October–November. In contrast, nectarivore richness was twice as high during April–May (six species) and more than twice as high during October–November (seven species) than during the periods from June through September (three species). Variability in frugi-granivore richness was intermediate with a minimum of six species during June–July and maxima of nine species during April–May and October–November (Fig. 1A).

Relative abundance.—Most species varied considerably in their relative abundance, the extreme case being the Sparkling Violetear (*Colibri coruscans*), which was common during December but absent from June through September (Table 1). Of the 19 year-round residents, 11 varied in their abundance by more than one category (Table 1). Thus, only eight species (23% of the entire core community) were fairly constant year round.

Overall abundance at the community level peaked during October–November (sum of abundance scores 75.0, mean 2.3) and was lowest during June–July (47.0, 1.9), and we found similar patterns at the guild level (Fig. 1B). When comparing species abundance scores between consecutive periods, none of the three guilds analyzed alone showed any significant variation (Table 2, results shown for insectivores only). Because frugi-granivores and nectarivores both depend upon plants as food resources, we pooled the data for the two guilds, which revealed a significant decrease from April–May to June–July ($Z = 2.41$, df = 15, $P = 0.016$) and a significant increase from June–July to August–September ($Z = 2.02$, df = 11, $P = 0.043$) in abundance (Table 2). We obtained similar results for the entire bird community, except that the decrease in abundance from October–November to December–January also was significant (Table 2). Note that we compared December–January to October–November of the next year, assuming between-year continuity.

Habitat specialists.—Three core species, the Tawny Tit-Spinetail (*Leptasthenura yanacensis*), the Giant Conebill (*Oreomanes fraseri*), and the Thick-billed Siskin (*Carduelis crassirostris*) are strongly specialized on *Polylepis* forest, and five species (Rusty-vented Canastero, *Asthenes dorbignyi*; Streak-fronted Thornbird, *Phacellodomus striaticeps*; Rufous-webbed Bush-Tyrant, *Polioxolmis rufipennis*; D'Orbigny's Chat-Tyrant, *Ochthoeca oenanthoides*; Rufous-bellied Saltator, *Saltator rufiventris*) show a marked affinity for this habitat (see Fjeldså and Kessler 1996). The

TABLE 1. Most of the 35 core species recorded in a *Polylepis* woodland at Sacha Loma, central Bolivia, varied in relative abundance (n.r. = not recorded; R = rare; U = uncommon; F = fairly common; C = common; A = abundant; see text for details) between 2-month survey periods, November 1999 to November 2000. At the guild level (ins = insectivore; fru = frugi-granivore; nec = nectarivore; car = carnivore), most insectivores were year-round residents, whereas the reverse was true for frugi-granivores and nectarivores. No data were collected in February and March. Taxonomy follows South American Checklist Committee (2002).

Species	Survey period					Diet
	Dec–Jan	Apr–May	June–July	Aug–Sept	Oct–Nov	
Ornate Tinamou (*Nothoprocta ornata*)	R	R	U-R	U	R	fru
Spot-winged Pigeon (*Columba maculosa*)	R	U	U-R	U	R	fru
Gray-hooded Parakeet (*Psilopsiagon aymara*)	R	n.r.	n.r.	n.r.	n.r.-U	fru
Yungas Pygmy-Owl (*Glaucidium bolivianum*)	n.r.	R	R	U	R	car
Sparkling Violetear (*Colibri coruscans*)	C-R	R	n.r.	n.r.	R	nec
Black-hooded Sunbeam (*Aglaeactis pamela*)	R	R	n.r.	n.r.	R	nec
Andean Hillstar (*Oreotrochilus estella*)	n.r.	R-U	R-U	F	U-R	nec
White-sided Hillstar (*O. leucopleurus*)	n.r.	n.r.	n.r.	R-U	U-n.r.	nec
Giant Hummingbird (*Patagona gigas*)	R	R	R	n.r.	R	nec
Red-tailed Comet (*Sappho sparganura*)	R	R	n.r.	n.r.	U	nec
Plain-breasted Earthcreeper (*Upucerthia jelskii*)	R	R-U	R	R	R	ins
Bar-winged Cinclodes (*Cinclodes fuscus*)	C	C-R	R	R	F-C	ins
Brown-capped Tit-Spinetail (*Leptasthenura fuliginiceps*)	n.r.	n.r.	n.r.	n.r.	R-U	ins
Tawny Tit-Spinetail (*L. yanacensis*)	C	C	C	C	C	ins
Cordilleran Canastero (*Asthenes modesta*)	R	n.r.	R	R	R-n.r.	ins
Rusty-vented Canastero (*A. dorbignyi*)	C	C-F	F	F	C	ins
Puna Canastero (*A. sclateri*)	F	U	R	F	F	ins
Streak-fronted Thornbird (*Phacellodomus striaticeps*)	F	C-F	U	U	F	ins
Puna Tapaculo (*Scytalopus simonsi*)	C	F	U	U	F-C	ins
White-throated Tyrannulet (*Mecocerculus leucophrys*	U	R-F	F	F	F	ins
Tufted Tit-Tyrant (*Anairetes parulus*)	R	U	U-F	U	R	ins
Rufous-webbed Bush-Tyrant (*Polioxolmis rufipennis*)	F-U	C-U	U-R	U	F	ins
D'Orbigny's Chat-Tyrant (*Ochthoeca oenanthoides*)	R	F	F	F	U	ins
White-browed Chat-Tyrant (*O. leucophrys*)	F	R	R	U	F-C	ins
Red-crested Cotinga (*Ampelion rubrocristatus*)	n.r.	U-n.r.	n.r.	n.r.	n.r.	fru
Andean Swallow (*Haplochelidon andecola*)	n.r.	n.r.	R-U	R	R-U	ins
Chiguanco Thrush (*Turdus chiguanco*)	U	C-F	U-F	F	F-C	fru
Giant Conebill (*Oreomanes fraseri*)	F	F	F	F	F	ins
Gray-bellied Flowerpiercer (*Diglossa carbonaria*)	F	n.r.-U	R	U	F-C	nec
Common Bush-Tanager (*Chlorospingus ophthalmicus*)	n.r.	n.r.	n.r.	n.r.	R	fru
Rufous-collared Sparrow (*Zonotrichia capensis*)	A-C	C-F	U-R	F	A	fru
Ash-breasted Sierra-Finch (*Phrygilus plebejus*)	A-C	C	C	A	A	fru
Rufous-bellied Saltator (*Saltator rufiventris*)	n.r.	R	R	n.r.	n.r.	fru
Thick-billed Siskin (*Carduelis crassirostris*)	U-F	R	n.r.	F	U-F	fru
Hooded Siskin (*C. magellanica*)	C	U-n.r.	n.r.	R	n.r.-F	fru

Tawny Tit-Spinetail and the Giant Conebill had constant abundance year round (Table 1). The Rusty-vented Canastero and the Streak-fronted Thornbird showed slight variation, being least abundant during the austral winter, whereas the D'Orbigny's Chat-Tyrant had its lowest abundance during December–January, and the Rufous-webbed Bush-Tyrant lacked a clear pattern. The Thick-billed Siskin was not recorded during June–July and peaked in abundance from August through January. The Rufous-bellied Saltator was recorded only during April–May and June–July when it was rare.

Noteworthy distributional record.—The occurrence of the White-sided Hillstar (*Oreotrochilus leucopleurus*) at Sacha Loma during the austral winter (Table 1) represents a northward range extension by about 400 km for this Andean species, which breeds mainly in Argentina and Chile and previously was known only from as far north as the department of Tarija

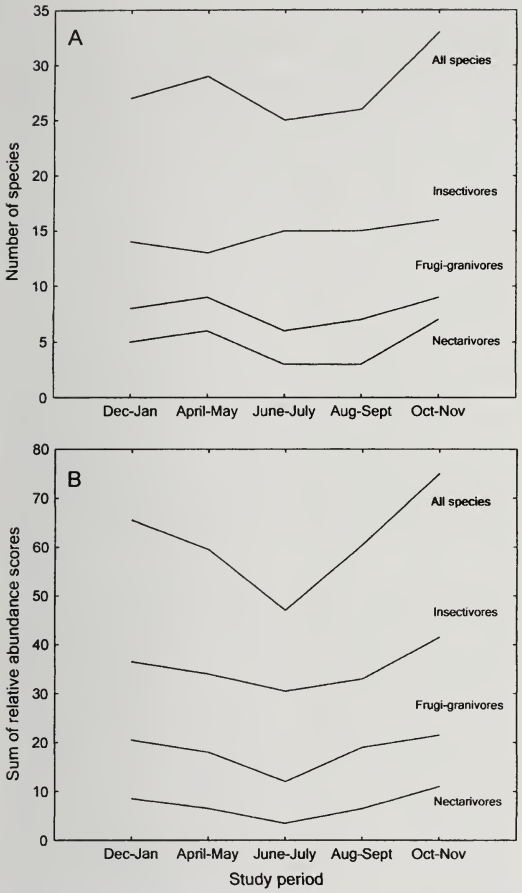

FIG. 1. Insectivores were the most temporally stable guild in the *Polylepis* bird community at Sacha Loma, central Bolivia, from November 1999 to November 2000, both in terms of (A) species richness and (B) relative abundance. No data were collected in February and March.

in southern Bolivia (Fjeldså and Krabbe 1990, Arribas et al. 1995, Fjeldså 1999). We first mist netted a male on 9 June 2000 in a nearby *Polylepis* patch, followed by a capture of a male on 7 August 2000 and subsequent observations until 16 October 2000 in the study fragment. Males of the White-sided Hillstar differ from those of the sympatric central Bolivian subspecies of the Andean Hillstar (*O. estella boliviana*) primarily by their blue-black rather than chestnut median stripe on the underparts (Fjeldså and Krabbe 1990).

These observations represent the first evidence that the White-sided Hillstar is an austral migrant. Although Marín et al. (1989) suggested that Chilean birds might migrate based on a single record in southern Antofagasta, de la Peña (1994) and Fjeldså (1999) mentioned only altitudinal movements for the species, and Parker et al. (1996) did not list the White-sided Hillstar as an austral migrant.

DISCUSSION

The insectivore guild was the most temporally stable at Sacha Loma both in terms of species richness and abundance, and we found no significant changes in abundance between seasons. In contrast, frugi-granivores and nectarivores combined showed considerable seasonal variation with a significant abundance low during the austral winter (June–July). Thus, our results indicate that Karr's (1976) hypothesis of highest seasonality in insectivores, which was derived from studies in tropical lowlands, does not apply to marginally tropical, high-elevation *Polylepis* forests. Seasonal variation at the community level largely reflected that of frugi-granivores and nectari-

TABLE 2. Frugi-granivores and nectarivores combined had a significantly low abundance in mid-winter (June–July) in a *Polylepis* woodland at Sacha Loma, central Bolivia, November 1999 to November 2000, as revealed by binomial sign tests comparing relative abundance scores between 2-month periods. This is reflected at the community level, whereas insectivores lacked significant variation. No data were collected in February and March.

	Insectivores (n = 16)		Frugi-granivores and nectarivores (n = 18)		All species (n = 35)	
Comparison	Z	P	Z	P	Z	P
Dec–Jan to April–May	0.0	1.000	0.29	0.773	0.20	0.838
April–May to June–July	0.60	0.546	2.41	0.016	2.35	0.019
June–July to Aug–Sept	0.0	1.000	2.02	0.043	2.12	0.034
Aug–Sept to Oct–Nov	1.58	0.114	1.03	0.302	1.54	0.124
Oct–Nov to Dec–Jan	1.06	0.289	1.58	0.114	2.01	0.044

vores, i.e., the two guilds dependent upon plants as food resources. The Sacha Loma bird community may be characterized as highly seasonal since only about one quarter of its core species were year-round residents with fairly constant abundances.

Relative abundance values do not necessarily reflect true abundances of species, but may be influenced by interspecific differences and seasonal changes in detectability. In the Bolivian Andes, vocal activity (and thus detectability) levels of forest birds tend to decrease considerably during the late rainy and first half of the dry season (SKH pers. obs.). Therefore, the question arises to what degree our data are biased by varying detectabilities of species. The relatively open vegetation structure of the *Polylepis* forest certainly reduced such biases, but even so, visually inconspicuous species that prefer to stay in dense vegetation or close to the ground, i.e., Ornate Tinamou (*Nothoprocta ornata*), Cordilleran (*Asthenes modesta*) and Puna (*A. sclateri*) canasteros, Puna Tapaculo (*Scytalopus simonsi*), and White-browed Chat-Tyrant (*O. leucophrys*), probably became less detectable during the late rainy season. The apparently low abundance of the Puna Tapaculo, a highly sedentary and almost flightless species (Fjeldså and Krabbe 1990), during the austral winter almost certainly is a result of reduced vocal activity during that season. However, except for the Ornate Tinamou, these visually cryptic species are insectivores. Thus, if seasonal changes in detectability biased our data, one would expect to find pronounced seasonal variation in abundance for insectivores rather than for frugi-granivores and nectarivores, which was not the case in Sacha Loma. In fact, the true seasonality in insectivores compared to frugi-granivores and nectarivores therefore is likely to be even less than what Fig. 1 indicates.

Several studies have shown that variations in abundance of birds over time are related to the availability of food resources (Karr 1976, Blake and Loiselle 1991, Loiselle and Blake 1991, Levey and Stiles 1992, Strong and Johnson 2001). Although we lack quantitative data on food supply, some comparisons can be made based on qualitative observations. Flowering and seeding of *Polylepis* trees, for example, is strictly seasonal. The first *Polylepis* trees had open flowers during July, and most trees were flowering during early August. Seeds still were present during late January and extended into February, but none were observed during mid-April. This pattern largely coincided with the abundance fluctuations of the Thick-billed Siskin, a habitat specialist that mainly feeds on flowers and seeds of *Polylepis* (Fjeldså and Krabbe 1990, Herzog et al. 2001). Other common woody plants such as *Berberis* (Berberidaceae) also started flowering during August, producing fruits and seeds during the rainy season.

Nectarivores primarily were observed at the flowers of two species, the annual vine *Salpichroa glandulosa* (Solanaceae) and the mistletoe *Tristerix penduliflorus* (Loranthaceae), a hemiparasite on *Polylepis* trees, although they also used other, less conspicuous flowers. Whereas *S. glandulosa* flowering was restricted to the rainy season, mistletoe flowers (and fruit) were available year round, but had their lowest abundance during the middle of the austral winter when species richness and abundance of nectarivores also was lowest. It is noteworthy that the Gray-bellied Flowerpiercer (*Diglossa carbonaria*) was the only nectarivore with year-round presence at Sacha Loma. This possibly was due to the feeding method of flowerpiercers, resulting in less specialization and allowing them to use a greater variety of flowers than any of the hummingbird species (Naoki 1998). Alternatively, *D. carbonaria* may have shifted to a more insectivorous diet during the dry season, given that Isler and Isler (1999) reported insect parts as stomach contents for this species.

Although the insectivore guild did not show significant abundance fluctuations, some insectivorous species nonetheless changed in abundance possibly in response to a variable food supply. The Bar-winged Cinclodes (*Cinclodes fuscus*) mostly forages along streams, on wet bogs or grassy glades, often in *Polylepis* woodlands (Fjeldså and Krabbe 1990, Fjeldså and Kessler 1996). This species was common during the rainy season when ephemeral aquatic microhabitats formed frequently, both in the *Polylepis* woodland and in the surrounding *puna* grassland, whereas it was rare during the dry season when even some springs near Sacha Loma dried up. This pattern coincides with anecdotal observations

of drastic body mass decrease in two banded *C. fuscus* individuals. When banded at the beginning of the dry season on 10 May 2000, the first bird had a body mass of 27.0 g and showed no traces of subcutaneous fat. The same bird was recaptured during the height of the dry season on 5 August 2000 weighing 20.5 g, 74% of its body mass in May. A second bird decreased in body mass from 31.5 g (again without signs of subcutaneous fat deposits) on 28 January 2000 to 27.0 g on 13 October 2000, suggesting that it reached a minimum during the dry season. Although we can not dismiss the possibility that those body mass losses were caused by other factors (e.g., a heavy parasite load), the most plausible explanation is a strong reduction in food supply and optimal foraging habitat during the dry season.

Of the eight *Polylepis* specialists recorded at Sacha Loma, six species showed variations in abundance, two of which left the fragment during part of the year. Those six species probably depend upon a certain degree of connectivity between suitable habitat patches, especially when inhabiting small fragments with more homogeneous environmental conditions than larger patches that cover greater elevational gradients. The need for habitat connectivity also might apply to some extent to the Giant Conebill, which, despite constant abundance during the study period, exhibited movements between fragments at Sacha Loma (Herzog et al. 2002b). Because anthropogenic fragmentation and deforestation of *Polylepis* woodlands due to excessive burning and grazing are ongoing (Fjeldså and Kessler 1996, Fjeldså 2002, Hensen 2002), studies on the metapopulation dynamics of *Polylepis* specialists are urgently needed to determine how they respond to such disturbance.

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APPENDIX

Differentiating between core species and visitors or vagrants is not always a straightforward process and may be disputable in some cases. Thus, we present a commented list of all species observed in the forest, directly at its edge, or flying over that were not considered core species of the *Polylepis* fragment at Sacha Loma, central Bolivia. Species exclusively observed in the surrounding *puna* grassland are not included.

Darwin's Nothura (*Nothura darwinii*). Observed only once during October 2000, when several birds were heard at forest edge.

Turkey Vulture (*Cathartes aura*). Single birds flying over the forest and *puna* during April, May, and August 2000.

Andean Condor (*Vultur gryphus*). Rare sightings of soaring birds during April, May, and July 2000.

Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*). Observed only during August 2000 in flight.

Red-backed Hawk (*Buteo polyosoma*). Seen in small numbers during most months in flight

or on ground in *puna* grassland. This species potentially may hunt in the forest fragment, but we never observed this behavior.

Mountain Caracara (*Phalcoboenus megalopterus*). This common *puna* species was observed in flight and on the ground in *puna* during most months.

Aplomado Falcon (*Falco femoralis*). We observed two birds hunting a passerine over *puna* during December 1999, and single birds were seen once each during May, June, July, and August 2000 either perched on top of a *Polylepis* tree or hovering over the fragment. This species may very occasionally prey on a *Polylepis* bird, but this alone does not warrant inclusion as a core species.

Blue-crowned Parakeet (*Aratinga acuticaudata*). We saw a flock of eight birds once during October 2000 in fast flight over the fragment.

Mitred Parakeet (*Aratinga mitrata*). We saw a flock of 8–10 birds once during December 1999 in fast flight over the fragment.

Mountain Parakeet (*Psilopsiagon aurifrons*). Small flocks in fast flight observed during May, July, August, and October 2000, but never observed perched in the forest.

White-collared Swift (*Streptoprocne zonaris*). A single bird circling relatively high above the forest in a flock together with the two *Aeronautes* species below during April 2000.

Andean Swift (*Aeronautes andecolus*). See White-tipped Swift (below).

White-tipped Swift (*Aeronautes montivagus*). A flock of about 50 birds circling together with two White-collared Swifts and about 50 Andean Swifts relatively high above the forest during April 2000.

White-vented Violet-ear (*Colibri serrirostris*). A single bird in pale juvenal plumage seen once during November 1999.

Great Sapphirewing (*Pterophanes cyanopterus*). Single birds seen twice in the forest during October 2000. Probably a rare visitor from the humid treeline zone.

Green-barred Woodpecker (*Colaptes melanochloros*). Two single birds observed during October 2000. Probably a rare visitor from deciduous forest at lower elevations.

Andean Flicker (*Colaptes rupicola*). Uncommon to common almost year-round (not recorded during June 2000) in the surrounding *puna* grassland, we observed this species only twice in the fragment, once at the edge (a copulating pair during November 1999) and once in the boulder field.

Rufous Casiornis (*Casiornis rufa*). We mist netted a single bird during August 2000. Probably a vagrant from deciduous forest at lower elevations.

Fawn-breasted Tanager (*Pipraeidea melanonota*). We mist netted a single bird during August 2000 and observed another during November 2000. Probably a vagrant.

Cinereous Conebill (*Conirostrum cinereum*). Two single birds seen during October 2000. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Plumbeous Sierra-Finch (*Phrygilus unicolor*). We mist netted a single bird during April 2000. Surprisingly, we did not observe this species in the *puna* grassland around our study site.

Rufous-sided Warbling-Finch (*Poospiza hypochondria*). Sightings of one (dispersing?) bird in juvenal plumage during May 2000 and of two individuals in adult plumage during October 2000. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Plain-colored Seedeater (*Catamenia inornata*). We mist netted a single bird during December 1999. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Golden-billed Saltator (*Saltator aurantiirostris*). A single bird heard once during November 1999. Probably a rare visitor from deciduous scrub and gardens near houses at lower elevations.

Black Siskin (*Carduelis atrata*). Four birds moving through scattered *Polylepis* bushes at the fragment edge during April 2000. Probably a rare visitor.

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SEASONAL AND ANNUAL VARIATION IN THE DIET OF BREEDING, KNOWN-AGE ROYAL TERNS IN NORTH CAROLINA

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ABSTRACT.—We investigated banded, known-age Royal Terns (*Sterna maxima*) in North Carolina during 1999 and 2000 to determine seasonal variation in their diet and any age-related correlations in foraging. Systematic observations of adults returning with food indicated that at least 18 families of fish, squid, and crustaceans were exploited. The most common forage species in both years were anchovies (Engraulidae), herring (Clupeidae), and drum (Sciaenidae). In 1999 we also monitored a sample of 48 color-banded, known-age breeding birds ranging in age from 6–17 years to assess variations in diet with age. We detected no age-related differences in Royal Tern prey size or selection; however, our sample was relatively small and further research is warranted. *Received 12 May 2003, accepted 5 October 2003.*

Royal Terns (*Sterna maxima*) have been increasing along the Atlantic coast of the eastern United States since protected, dredge material islands with suitable nesting habitat were created in the 1960s (Parnell et al. 1997). The population size of nesting adults in North Carolina has fluctuated over the last few decades, ranging from as low as 9,755 nests during 1977 to as high as 17,029 nests during 1983 (Parnell et al. 1997). During the 1960s an extensive banding effort of Royal Tern fledglings was initiated along the Atlantic coast (Van Velzen and Benedict 1972) and has been continued by J. Weske annually to the present at colonies in Maryland, Virginia, and North Carolina. These efforts have resulted in the world's only known-age population of breeding Royal Terns. However, until now, studies of age-related variables in correlation with life history strategy, diet, and foraging ecology of Royal Terns have been limited to Buckley and Buckley's (1974) comparison of juveniles to adults.

Most seabirds are long lived and have adaptations to maximize reproductive success and survivorship in a variable marine environment (Furness and Monaghan 1987, Ricklefs 1990, Hamer et al. 2001). Royal Terns display reproductive traits that warrant investigation of age-related differences in foraging ecology, such as reduced clutch size, extended parental care, delayed sexual maturity, and long life span (Buckley and Buckley 1972). Most monogamous pairs lay one-egg clutches, although some occasionally lay two-egg clutches (Dunn 1972; Buckley and Buckley 1972, 2002). Moreover, adults have been observed feeding their young up to six months after hatching (Buckley and Buckley 1974, Erwin 1977), a behavior that likely evolved as a response to difficulty in locating and capturing prey and the time necessary for young birds to become proficient at foraging (Ashmole and Tovar 1968, Hamer et al. 2001).

Here, we investigated the diet of known-age Royal Terns in the Lower Cape Fear River, North Carolina, during two breeding seasons. Our primary objectives were to document for the first time in this species any seasonal variations in colony diet and prey size. In addition, we used systematic observations of marked, known-age adults to address the possible correlation of age with foraging behavior. We based this portion of our study on the premise that Royal Tern reproductive success improves with age, and that age correlates with previous breeding experience and increased foraging efficiency, as has been shown in other larids (Coulson and Horobin 1976, Ryder 1981, Pugesek and Diem 1983, Nisbet et al. 1984, Pyle et al. 1991, Sydeman et al. 1991, Galbraith et al. 1999). As such, older Royal Tern parents should return with higher quality prey for their chicks compared to younger birds.

METHODS

Study area.—We studied two colonies of Royal Terns on Ferry Slip (34° 02′ N, 77° 56′

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W) and South Pelican (33° 56′ N, 77° 58′ W) islands in the Lower Cape Fear River from mid-May to early August, 1999 and 2000. Both islands were formed from dredge material and are managed by the National Audubon Society. In 1999, Ferry Slip was moderately vegetated with grasses, forbs, and shrubs. A mixed Royal and Sandwich tern (*Sterna sandvicensis* Latham) colony on Ferry Slip was comprised of approximately 1,600 nests (132 were Sandwich Tern) in three subunits. This colony was substantially reduced in 2000 (to <200 nests), possibly by plant succession in the nesting habitat (EJW and SDE pers. obs). Most Royal and Sandwich terns in the Lower Cape Fear region nested on South Pelican during 2000, where a colony of >4,300 nests (1,365 were Sandwich Tern) formed in a large contiguous area of bare sand. Five adults color banded on Ferry Slip in 1999 were found nesting on South Pelican in 2000 indicating that at least some individuals from the former colony moved to South Pelican.

Diet observations.—We assessed Royal Tern diet during 15-min observation periods from a stationary point within 20 m of the crèche from 05:00–19:00 EST using 8 × 42 binoculars. All observations were conducted by EJW each year during chick rearing from late May or early June, when most chicks were hatching, until mid- to late July, when most chicks begin flying. Prey carried in the bill of adults flying directly above a portion of the colony were identified in most cases by visible characters; otherwise, they were categorized as unidentified finfish or unknown. Prey size was estimated relative to tern bill length (mean = 63.9 mm ± 2.4 SD, $n = 46$). Size was divided into five categories: <0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, and >2 × bill length (BL).

We conducted observations so that four tidal stages (ebb, low, flood, and high) were evenly represented in time spent observing prey. We also divided the season into 4–5 biweekly periods that corresponded to the full and new moon, so that spring tides were in the middle of each time period. We did not compare prey between years due to better prey identification ability during the second year.

Known-age adult observations.—In 1999, we captured 48 known-age birds, ranging from 6–17 years old, in a mist net placed at the edge of the colony and added a plastic color band combination corresponding to age (right leg) and individual (left leg) and marked their breast feathers with saturated (1.2%) picric acid to facilitate field observations; weight was recorded with a Pesola scale to the nearest 1.0 g. This procedure was not repeated in 2000 to limit disturbance to the colony.

We observed the colony for marked birds during both morning and afternoon at all tidal stages. When a marked bird carrying prey was seen, time of day, age class, and prey type and size were noted. Number and age of chicks could not be determined for this part of the study because we did not locate the nest of each marked bird. Because of small sample sizes for birds of different ages, the data were combined into three age classes: young (6–8 years old), middle-aged (9–11 years), and old (12–17 years) because most birds in this species do not begin breeding until age 5–6 (Buckley and Buckley 2002). Thus, the young age class would include birds with only 1–3 years of breeding experience.

Statistical analyses.—We analyzed all diet data, except for known-age diet results, with ANOVA when assumptions of normality of residuals and homogeneous variance were met. When assumptions of ANOVA were not achieved, we used Kruskal-Wallis (when df ≥ 2) or Wilcoxon (when df = 1) tests reported as χ^2 values. We used pairwise correlations to test for association between season and diet. We used Fisher's exact test to compare categories of prey composition and prey size among age classes in 1999 (Sokal and Rohlf 1969). All statistical analyses were completed with the JMP IN software program (Sall and Lehman 1996).

RESULTS

We observed a total of 2,310 and 4,148 prey items during 14.25 and 20.00 h of observations during 1999 and 2000, respectively (Table 1). In both years, the majority of identified prey remains were anchovy, herring, and drum. In 1999, fewer prey were observed than in 2000. The percentage of unidentified finfish to total prey observed was 46% in 1999 and 18% in 2000. Prey type fluctuated seasonally (Fig. 1; see statistical tests below for each major prey group), but the most common prey

TABLE 1. Taxa of Royal Tern prey observed at two colonies in the Lower Cape Fear River, North Carolina in 1999 and 2000 showing the diversity in prey consumed by this species. Numbers of observations are given for each prey item with percent of total prey in parentheses.

Prey	1999	2000
Engraulidae (anchovies)		
Anchoa hesetus, *A. mitchilli*	290 (12.6)	495 (11.9)
Clupeidae (herrings)		
Brevoortia tyrannus, *Alosa* spp.	265 (11.5)	843 (20.3)
Sciaenidae (drums)		
Micropogonias undulatus, *Leiostomus xanthurus*, *Stellifer lanceolatus*, *Bairdiella chrysoura*, *Cynoscion* spp., *Sciaenops ocellatus*	296 (12.8)	1,025 (24.7)
Mugilidae (mullets)		
Mugil cephalus	182 (7.9)	31 (0.8)
Pleuronectiformes (unidentified)	2 (0.1)	72 (1.7)
Cynoglossidae (tonguefishes)		
Symphurus spp.	38 (1.7)	171 (4.1)
Sparidae (porgies)		
Lagodon rhomboides, *Archosargus probatocephalus*	32 (1.4)	36 (0.9)
Carangidae (jacks)		
Caranx spp., *Seriola* spp.	9 (0.4)	94 (2.3)
Gadidae (hakes)		
Urophycis spp.	6 (0.3)	6 (0.1)
Trichiuridae (cutlassfish)		
Trichiurus lepturus	2 (0.1)	24 (0.6)
Triglidae (searobins)		
Prionotus spp.	2 (0.1)	7 (0.2)
Synodontidae (lizardfish)	1 (0.04)	8 (0.2)
Stromateidae (butterfish)		
Peprilus triacanthus	—	11 (0.3)
Haemulidae (grunts)	—	3 (0.1)
Pomatomidae (bluefish)		
Pomatomus saltatrix	—	17 (0.4)
Syngnathidae (pipefishes)	3 (0.1)	7 (0.2)
Ophichthidae (eels)	8 (0.4)	21 (0.5)
Loliginidae (squids)	32 (1.2)	109 (2.6)
Penaeidae (shrimps)		
Penaeus spp.	58 (2.5)	256 (6.2)
Brachyura (crabs)	14 (0.6)	85 (2.1)
Unidentified finfish	1,064 (46.1)	759 (18.3)
Unknown	6 (0.3)	68 (1.6)

proportions did not vary with tidal stage during both years (Kruskal-Wallis test, $\chi^2 = 0.64$, df = 3, $P = 0.28$).

Proportion of anchovies fed to chicks decreased across time periods during both years (1999: $\chi^2 = 27.6$, df = 3, $P < 0.0001$; 2000: $\chi^2 = 56.0$, df = 4, $P < 0.0001$) and was inversely correlated with date in both 1999 ($r_{57} = -0.59$, $P < 0.0001$) and 2000 ($r_{80} = -0.74$, $P < 0.0001$). Drum varied among time periods in both years (1999: $\chi^2 = 14.0$, df = 3, $P < 0.003$; 2000: $\chi^2 = 22.1$, df = 4, $P < 0.0002$) and were observed more per trial toward the end of the 1999 season ($r_{57} = 0.41$, $P < 0.002$). In 2000 there was no significant correlation between drum and date ($r_{80} = 0.18$, $P = 0.10$). Herring decreased by time period (1999: $\chi^2 = 9.8$, df = 3, $P = 0.021$; 2000: $F_{3,79} = 2.4$, $P = 0.059$) and date in 1999 only ($r_{57} = -0.37$, $P = 0.005$). Number of shrimp (Penaeidae) identified per trial was positively correlated with date in 1999 ($r_{57} = 0.30$, $P = 0.022$) and 2000 ($r_{80} = 0.22$, $P = 0.048$) and increased among time periods during both years (1999: $\chi^2 = 7.7$, df = 3, $P = 0.049$; 2000: $\chi^2 = 25.6$, df = 4, $P < 0.0001$). During 1999 mullet did not vary significantly among time periods ($\chi^2 = 6.3$, df = 3, $P = 0.10$). During 2000, Tonguefish (Cynoglossidae) abundance in the observed prey was not

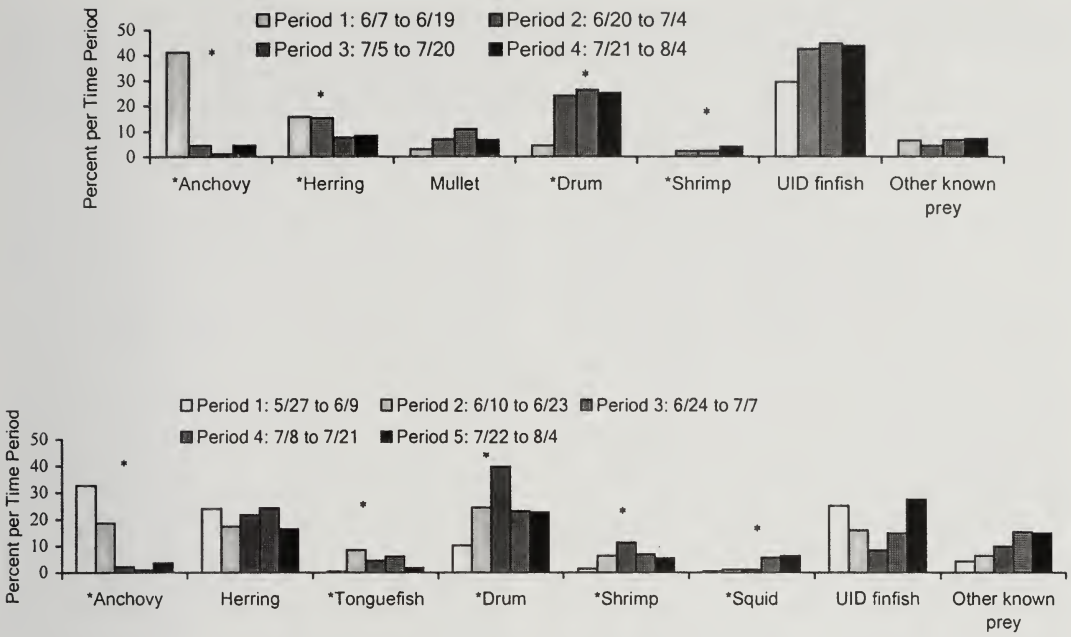

FIG. 1. Weekly variation in the proportion of major prey items of Royal Terns identified during 15-min periods. (Top) 1999: n = 2,310. (Bottom) 2000: n = 4,148. Asterisk indicates significant difference among periods.

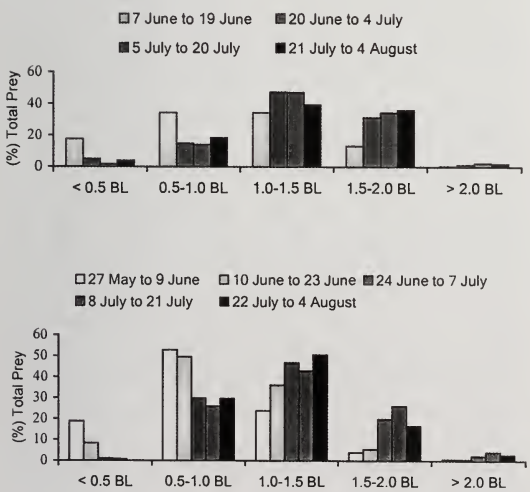

FIG. 2. Percentage of prey brought to Royal Tern chicks by size categories estimated relative to adult bill length (BL). Prey size increased significantly among time periods throughout the breeding season; (top) 1999: Pearson χ^2 = 169.81, df = 12, $P < 0.0001$ and (bottom) 2000: χ^2 = 896.81, df = 16, $P < 0.0001$.

significantly correlated to date (r_{80} = 0.04, P = 0.71), but among time periods proportion of tonguefish varied considerably (χ^2 = 23.2, df = 4, $P < 0.0001$). Squid (Loliginidae) were observed in 2000, but mostly at the end of the season (by periods: χ^2 = 42.6, df = 4, $P <$ 0.0001; by date: r_{80} = 0.60, $P < 0.0001$).

The size of prey increased seasonally during both 1999 and 2000 (Fig. 2). For 1999, during periods two through four, prey sizes from 1–2 BL were most prevalent (65–75% of all prey). In 2000, during periods one and two, prey items were mostly 0.5–1.0 BL (53% and 49%, respectively). Most prey observed during 2000 were between 0.5–1.5 BL (69–86%).

In 1999, the 48 marked, known-age birds included 11 in the young, 13 in the middle, and 24 in the old age classes. These birds were observed feeding chicks for a total of approximately 54 h. Prey size (Fisher's exact test, n = 127, P = 0.32) and type (Fisher's exact test, n = 126, P = 0.092) did not differ significantly among adult age classes with an analysis of eight prey categories (anchovy, herring, drum, crab, shrimp, mullet, other

thin-bodied finfish, and other deep-bodied finfish).

DISCUSSION

Prior to now, little research has been conducted on the diet of Royal Terns. Buckley and Buckley (1972) found that anchovy, silversides (Menidia) and menhaden (Brevoortia) were the most common prey at colonies in North Carolina and Virginia, but provided no quantitative data. McGinnis and Emslie (2001) found that Royal Tern chick diet, observed primarily at one colony in North Carolina, was comprised of 41% drum, porgies (Sparidae), and mullet; 30% herring, jacks (Carangidae), and mackerel (Scombridae); and 9% anchovies. These results are consistent with our findings. A study in Argentina (Quintana and Yorio 1997) found that Royal Terns breeding at Punta León, Patagonia, fed primarily on anchovy (*Engraulis anchoita*) in 1992 (>60% of 523 prey items observed), but switched to Fueguian sprat (*Sprattus fueguensis*, >30%) in 1993.

We found Royal Tern prey type to vary seasonally, as in other tern species during breeding (Safina and Burger 1989, Safina et al. 1990, Shealer 1998). The decline in anchovies after the first two weeks after hatching in both years suggests that parents either were choosing to feed their hatchlings a small, thin-bodied prey item, or anchovy availability near the lower estuary was greater early in the season and then declined by late June. Common anchovies of the Lower Cape Fear River estuary and coastal waters include striped (*Anchoa hepsetus*) and bay anchovy (*A. mitchilli*). These species occur year round in this estuary and spawn mostly at night offshore during late spring and summer (Zastrow et al. 1991, MacGregor and Houde 1996). Anchovy oceanic spawning coincides with tern nesting, and anchovy availability in the marine habitat may contribute to the onset of Royal Tern courtship along the Atlantic coast.

Later in the season, terns rely on a greater variety of larger-sized prey as their chicks increase in size. A trend repeated in both years was an increase in the proportion of drum and shrimp in mid- to late June. This trend coincides with the growth and movement of juvenile drum (e.g., *Leiostomus xanthurus* and *Micropogonius undulatus*) and brown shrimp (*Penaeus aztecus*) from upriver to more saline water (Schwartz et al. 1979). Both of these prey appeared in Royal Tern diets more during 2000 than in 1999. However, because observer identification skills improved markedly between 1999 and 2000, drum and other forage species may be underrepresented if categorized as unidentified finfish in 1999. Alternatively, if the shift in Royal Tern diet from mullet in 1999 to tonguefish and squid in 2000 is real, it suggests that prey switching occurred perhaps due to changing availability of specific forage species.

Common Terns (*Sterna hirundo*) show sexual variation in chick feeding, and there is evidence that males feed chicks more frequently than females in freshwater conditions where predictability of prey is greater (Wagner and Safina 1989, Burness et al. 1994). Sexes were not distinguished in our study, and if Royal Terns follow this pattern in estuarine habitats, then adult sex may explain some of the variation in our results.

Observations of marked, known-age birds failed to indicate any variation in prey size or type among three age classes. This result may be due to the relatively small sample size and number of observations we completed in 1999, as well as the large proportion of unidentified finfish that year; additional investigations are warranted. Because Royal Tern chicks crèche two to three days after hatching (Buckley and Buckley 2002), more detailed observations would necessitate restricting chicks at the nest and conducting focal observations (Erwin 1977).

Our results provide the most detailed analysis of Royal Tern diet now known (see review by Buckley and Buckley 2002) and indicate considerable variation in prey choice, although this species depends largely on only a few taxa for the bulk of its diet. We believe the seasonal variability in diet of Royal Terns is a response to seasonal productivity of forage species and abiotic factors (e.g., tidal stages). We predict that chick growth and mean fledgling weights also will vary seasonally in response to these conditions and that, with additional data, Royal Terns could be used as an indicator for relative abundance of fish stocks of preferred prey, as has been demonstrated for the Arctic Tern (*Sterna paradisaea*; Monaghan et al. 1989a, 1989b), Northern Gannet

(*Sula bassanus*; Montevecchi et al. 1988), Atlantic Puffin (*Fratercula arctica*; Barrett 2002) and Common Guillemot (*Uria aalge*; Burger and Piatt 1990, Monaghan et al. 1994).

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VOCALIZATIONS OF THE TUAMOTU SANDPIPER, *PROSOBONIA CANCELLATA*

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ABSTRACT.—The biology of the endangered Tuamotu Sandpiper (*Prosobonia cancellata*) is essentially unknown. We analyzed vocalizations from presumed adult individuals and pairs, and family groups, recorded in French Polynesia during March 1990 and 2003. We recognized three types of vocalizations. Presumed adults uttered types I and II. These were brief (about 30–40 and 20–120 ms, respectively) and simple in structure (increasing then decreasing in frequency) but harmonically rich, with most energy in the second or third harmonics (peak fundamental frequency was about 775–1,380 Hz), as in some other Scolopacidae. Higher harmonics reached unusually high frequencies for a scolopacid (approaching 14 kHz). Call types I and II were uttered singly or as couplets, triplets, or longer sequences. Type III calls were longer (about 115–470 ms), of narrower bandwidth, and with modulations of a carrier frequency that decreased from about 1,925 to 1,305 Hz; they were given by a presumed family group and may represent calls of dependent young birds. Harmonic richness and variation in frequency and temporal variables within call types are consistent with a short range communication system. *Received 14 November 2002, accepted 31 October 2003.*

The Tuamotu Sandpiper (*Prosobonia cancellata*) is one of the most highly endangered and least known of the world's shorebird species. It is the only extant member of the genus, the other species becoming extinct by the late 1800s (Zusi and Jehl 1970, Holyoak and Thibault 1984, Sibley and Monroe 1990, Piersma 1996, van Gils and Wiersma 1996). A tropical distribution, atoll habitat, and sedentariness are unique among extant scolopacids, so information about the natural history and behavior of *Prosobonia* likely will be informative about both adaptations and phylogenetic relationships. Avian vocalizations are a traditional source of adaptive and phylogenetic information about nonpasserines and passerines (Irwin 1996, Kroodsma and Miller 1996, Salzburger et al. 2002). We analyzed available audio recordings and here present the first account of the species' vocalizations, offer provisional behavioral and evolutionary interpretations, and suggest directions for future research.

METHODS

Vocalizations were recorded in French Polynesia by R. and J. Seitre on Anuanu Raro (20° 17′ S, 143° 19′ W; 13 March 1990) and Morane (23° 06′ S, 137° 04′ W; 17 March 1990), and by EV on Morane (8 March 2003). Four sequences of vocalizations were recorded by the Seitres: bird in tree on Anuanu Raro (Seitres' sample 1; n = 24 calls), same bird in flight (Seitres' sample 2; n = 5), same bird on ground (Seitres' sample 3; n = 88), and a group of four to five birds on Morane (Seitres' sample 4; n = 30). For Seitres' samples 1–3 the vocalizing bird was alert to the presence of human observers and seemed to be calling as a result. The group on Morane may have been a family and was noted as giving "contact" calls. EV recorded two sequences from a pair (individuals A, B) for a total of 214 calls. Upon analysis, some calls appeared to differ from those that could be ascribed to the two birds (although they may have been different call types from those individuals), so these were included only in overall statistical summaries. The following is an excerpt from EV's notes: "They were clearly aware of my presence, watching me while perched in *Pandanus tectorius* trees and on *Scaevola taccada* shrubs. At times only one of the birds was close by [= sample 1], but during one sequence [= sample 2] the second bird approached more closely and the birds followed each other while moving among the vegetation. Some of the calls seemed to be a response to my presence, but some seemed to be directed at the other pair member, particularly when both birds were close by. Calls

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TABLE 1. Variation between and within call types I and II: descriptive statistics of the vocalizations of the Tuamotu Sandpiper, *Prosobonia cancellata*, recorded in French Polynesia in 1990 (by R. and J. Seitre) and 2003 (by E. VanderWerf). Call type I differed significantly between recordists in duration and peak frequency (*t*-tests, $P < 0.001$ for each comparison), and in Seitres' samples, call types I and II differed significantly from one another in duration and peak frequency (*t*-tests, $P < 0.001$ for each comparison).

	Call duration (ms)		Peak frequency in F0 (Hz)	
Sample (*n*)[a]	Mean ± SD	Range	Mean ± SD	Range
Call type I				
Seitre 3 (91)	65.2 ± 10.78	45–122	1,085 ± 43.2	1,005–1,235
VanderWerf 1A (94)	47.1 ± 11.64	22–80	1,194 ± 83.0	1,034–1,378
VanderWerf 1B (6)	73.5 ± 17.42	51–102	1,264 ± 76.0	1,163–1,357
VanderWerf 1 total (101)	48.6 ± 13.44	22–102	1,198 ± 83.5	1,034–1,378
VanderWerf 2A (84)	55.0 ± 12.24	33–86	1,247 ± 61.0	1,077–1,378
VanderWerf 2B (20)	51.6 ± 12.49	33–82	1,177 ± 84.6	991–1,337
VanderWerf 2 total (113)	53.7 ± 12.06	33–86	1,228 ± 72.4	991–1,378
VanderWerf all (214)	51.3 ± 12.96	22–102	1,214 ± 79.1	991–1,378
Call type II				
Seitre 1 (24)	39.3 ± 4.98	31–53	813 ± 28.0	775–861
Seitre 2 (5)	30.6 ± 8.44	21–42	884 ± 51.4	804–919

[a] VanderWerf's samples A and B are different individuals.

were given while perched and occasionally in flight."

Recordings were digitized at 22,050 (Seitres' samples) or 44,100 (EV's samples) Hz from recordings on cassette audiotapes, which were either original recordings made in the field with a dictaphone by the Seitres, or original recordings made on Sony professional 60-min tape by EV using a Marantz PMD222 cassette tape recorder and a Sennheiser ME66 shotgun microphone. We analyzed samples with Raven ver. 1.0 (Cornell Laboratory of Ornithology), or CSL 4100 or Multi-Speech 3700 (Kay Elemetrics Corporation). We measured temporal and frequency variables in Raven on spectrograms produced with (a) filter bandwidth of 141 Hz and grid resolution of 2.90 × 86 Hz, and (b) filter bandwidth of 35 Hz and grid resolution of 11.6 × 21.5 Hz, respectively. Maximal frequency of the fundamental frequency (of call types I and II) and initial and terminal frequencies (of call type III) also were measured, using Raven's "Max Frequency" function for a selection of the spectrogram area of interest. We measured intercall intervals between successive calls by individual birds. Not all call variables or intercall intervals could be measured, so reported sample sizes vary.

Spectrograms of type III calls were prepared over a logarithmic scale of 0.5–500 kHz. A logarithmic scale graphically simulates a range of analyzing filter bandwidths, and was best for revealing various acoustical properties of this call type (Marshall 1964, 1977; Marshall and Sugardjito 1986; Miller 1992).

Call type I differed significantly between recordists: calls recorded by EV were significantly briefer and of higher peak frequency (Table 1), perhaps because of EV's superior recording system. However intercall intervals (for intervals <3 s in duration) did not differ significantly (Kruskal-Wallis test: $Z = 0.33$, $P = 0.56$). Therefore samples from both recordists were combined for the latter variable.

RESULTS

Two broad classes of vocalizations were evident: brief, harmonically rich calls, with most energy in the second or third harmonic (call types I and II), and long, narrow band calls of descending frequency with moderate harmonic structure and most energy in the fundamental frequency (call type III). Call types I and II were either brief (Seitres' samples 1 and 2) or long (Seitres' sample 3 and EV's samples).

Type I calls were the most common in the recordings. They were uttered singly or as couplets, triplets, or longer sequences. Intercall intervals ranged from 64 ms to 8.5 s (mean = 805 ms, median = 555 ms, $n = 250$)

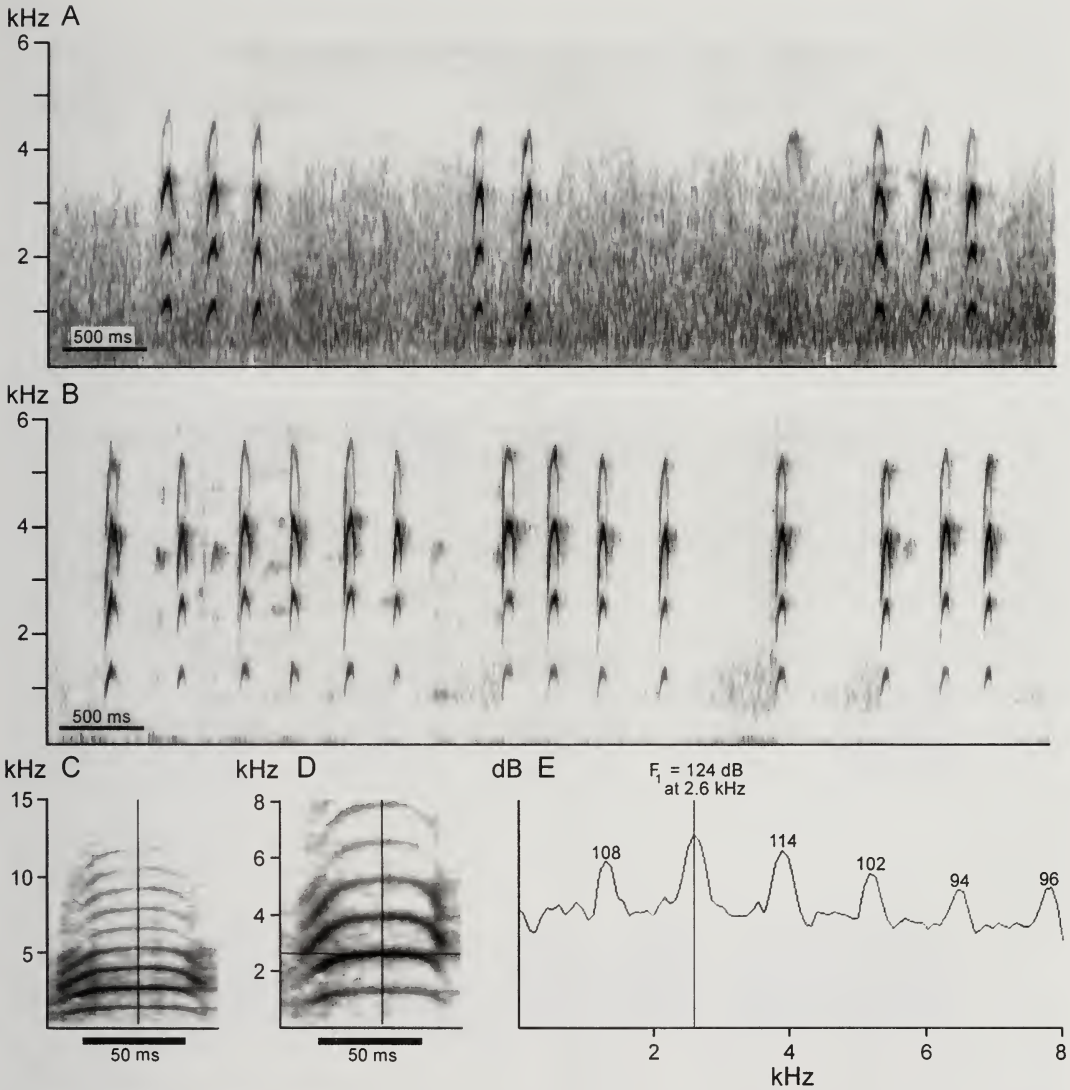

FIG. 1. Rhythmicity is common (A, B) and a broad frequency spectrum with most energy in the second or third harmonics is ubiquitous (C–E) in type I calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre (A) and in 2003 by E. VanderWerf (B–E). (A, B) Sequences of calls uttered by single birds (spectrograms produced in CSL 4100: Blackman window, analyzing filter bandwidth = 126 Hz). (C–E) Single call shown as spectrograms with different frequency ranges and (at the point marked by a vertical line in spectrograms C and D) as a power spectrum (spectrograms produced in Raven: Blackman window, filter bandwidth = 141 Hz, grid resolution = 2.9 ms × 86 Hz). (E) Unlabelled values above peaks are in dB.

in the typically skewed manner of interval data (skewness = 4.03). Eight of the intervals were >3 s in duration (five 3–4 s, two 4–5 s, one >8 s). For intervals <3 s long, mean = 687 ms and median = 540 ms (n = 242). The presence of rhythmic calling in many sequences is reflected in the predominance of short intercall intervals: 4.0% for <200 ms; 25.2% for 200–299 ms; 8% for 300–399 ms; and progressively declining values for greater intervals. Examples of rhythmic calling are apparent in Fig. 1A, B.

Other distinctive attributes of type I calls are the large frequency range (to nearly 14

kHz in some of EV's recordings; the frequency range was smaller in Seitres' samples, likely due to the poor recording equipment used), rich harmonic structure, and peak energy in second or third harmonics (Fig. 1C–E). Type I calls were brief, with means of 59–65 ms in Seitres' samples and 47–51 ms in EV's samples (Table 1). They were structurally simple, with most showing a gradual increase in frequency to a peak around the midpoint of the call, then a gradual decrease, and with few elaborations except position of the peak frequency and quasi-rhythmic frequency modulation. The transition point in frequency in brief calls was little more than a sharp inflection point, but in longer calls frequency increased then decreased slowly, and sometimes frequency changed little over much of the call (Fig. 2p, q). The mean peak frequency of the fundamentals were 813–1,023 Hz (Seitres' samples) and 1,194–1,214 Hz (EV's samples).

Peak frequency occurred at or just past the midpoint in most type I calls, but preceded the midpoint in some (Fig. 2f–i). The frequency contour was usually simple but modulations of the carrier frequency sometimes occurred at the beginning (Fig. 2l, second call), middle (Fig. 2g–i), or throughout (Fig. 2m). Other variations occurred in duration and (between some individuals) in whether peak frequency occurred in the second or third harmonic (e.g., the calls of birds A and B in Fig. 3l).

Within Seitres' samples, call type II was significantly shorter than and of lower peak frequency than call type I (Table 1). The two call types were similar in being harmonically rich and consequently in covering a broad frequency range (Figs. 2, 3a–f). The lower frequency range evident in Seitres' sample of type II calls likely resulted from the poor recording equipment used, as noted. Patterns of frequency change and frequency variations were similar to those noted for call type I (Fig. 3a–f). However, recordings of this call type were of poor quality and some details of acoustic structure may not have been apparent.

Temporal and frequency variation in call types I and II were substantial (Table 1). For example, durations varied nearly three-fold within Seitres' sample of type I calls, and more than two-fold within Seitres' samples of type II calls; peak frequency varied by about 10–20% within Seitres' samples. Even greater variation characterized EV's samples (overall, five-fold differences in duration and about 40% variation in peak frequency). Nonrandom variation within samples also was apparent. In the long sequence of calls in Seitres' sample of type I calls, the first five calls were 101, 125, 112, 94, and 74 ms long, the eighth was 80 ms long, and the other 82 calls ranged from 43–70 ms in duration. In the same sample, the second and third calls had the highest peak frequency.

Type III calls (n = 30) were distinctive (Fig. 3). They were longer, higher in frequency, and harmonically less rich than call types I or II. In addition, most energy was in the fundamental frequency, not in higher harmonics. Mean values were 280 ms ± 67.7 SD duration (range 113–471 ms) with initial frequency of the fundamental at 1,926 Hz ± 402.2 SD (range 1,467–3,027 Hz), terminal frequency of the fundamental at 1,305 Hz ± 262.1 SD (range 947–2,360 Hz), and frequency range of the fundamental at 623 Hz ± 279.5 SD (range 253–1,440 Hz). In the sample, 27 calls began at frequencies <2,100 Hz, three calls began at >2,700 Hz, and no intermediate values were recorded.

Some type III calls began with complex modulations (Fig. 3g, m) or sharp decreases in frequency (Fig. 3h, k, l). The carrier frequency often declined monotonically but exceptions were numerous (e.g., frequency reversals and shifts). Quasi-rhythmic modulations of the carrier frequency were common over the course of each call. Calls ended variably in the rate and pattern of frequency decrease, and some ended with pronounced downward frequency sweeps (Fig. 3h, j). The second harmonic usually was evident but higher harmonics were only variably apparent throughout part or all of the calls.

DISCUSSION

We provisionally identified three call types of *Prosobonia* based on our limited recordings. The species' repertoire almost certainly is larger, as in other scolopacids (Miller 1984, 1992). However, repertoires of species that communicate mainly over short distances may show much structural intergradation and few distinct structurally defined classes (Green 1975, Marler 1976, Green and Marler 1979).

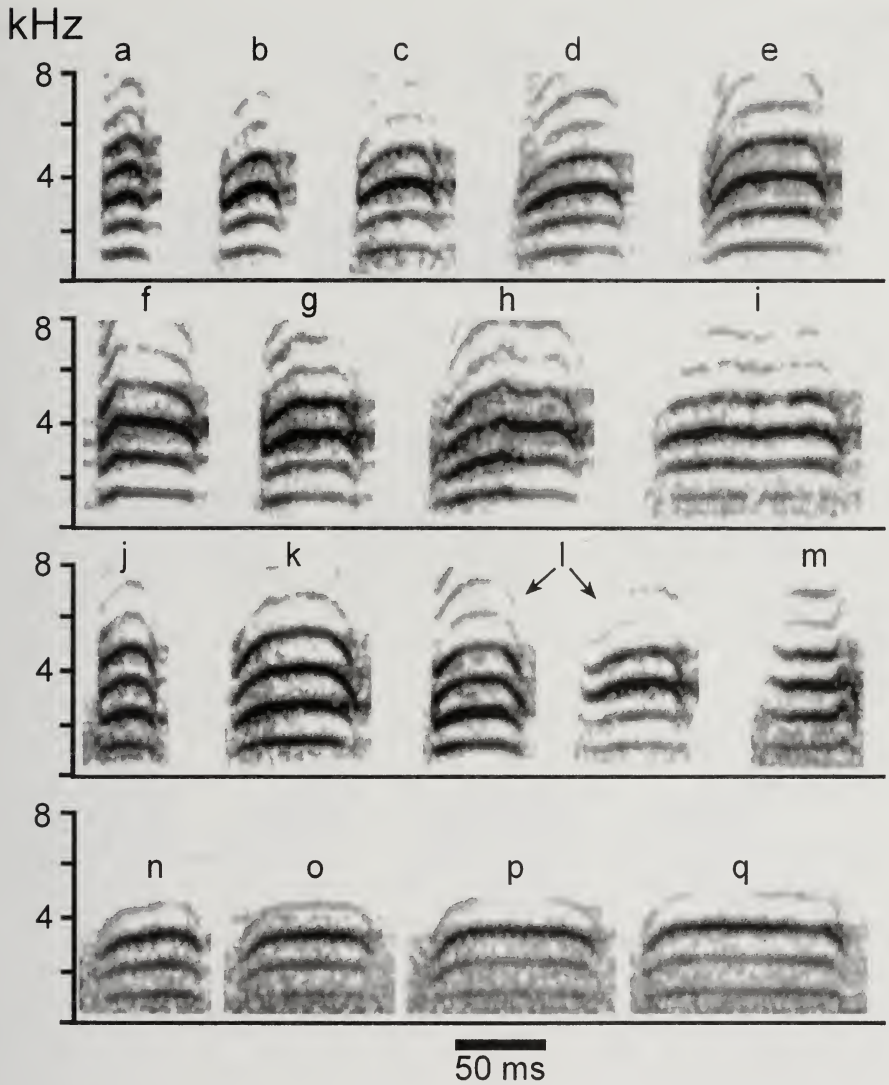

FIG. 2. Much fine scale variation is present in temporal and spectral features of type I calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre (n–q) and in 2003 by E. VanderWerf (a–m; successive calls by birds A and B are shown in spectrogram l). Spectrograms were produced in Raven (Blackman window, filter bandwidth = 223–226 Hz, grid resolution = 1.45–1.47 ms × 86 Hz).

Among shorebirds, the Northern Jacana (*Jacana spinosa*) provides an example of structural integradation (Jenni et al. 1974, Mace 1981, Jenni and Mace 1999); *Prosobonia* may be another example, judging by its type I and II calls.

Call type I (and perhaps type II) presumably is the one described by most authors. Hayman et al. (1986:337) stated that "a soft high-pitched whistle is the only call described." Holyoak and Thibault (1984:77) remarked that "the most common and characteristic call is a series of high-pitched whistled sounds, often repeated for a long time when the bird is perched or in flight" (EHM translation). Other descriptions include "a high pitched piping sound that [the bird] keeps up practically all day" (Bruner 1972:58), "a soft 'pew' 'pew' squeaking call [given] almost continually" (Holyoak 1973:28), and "a high-

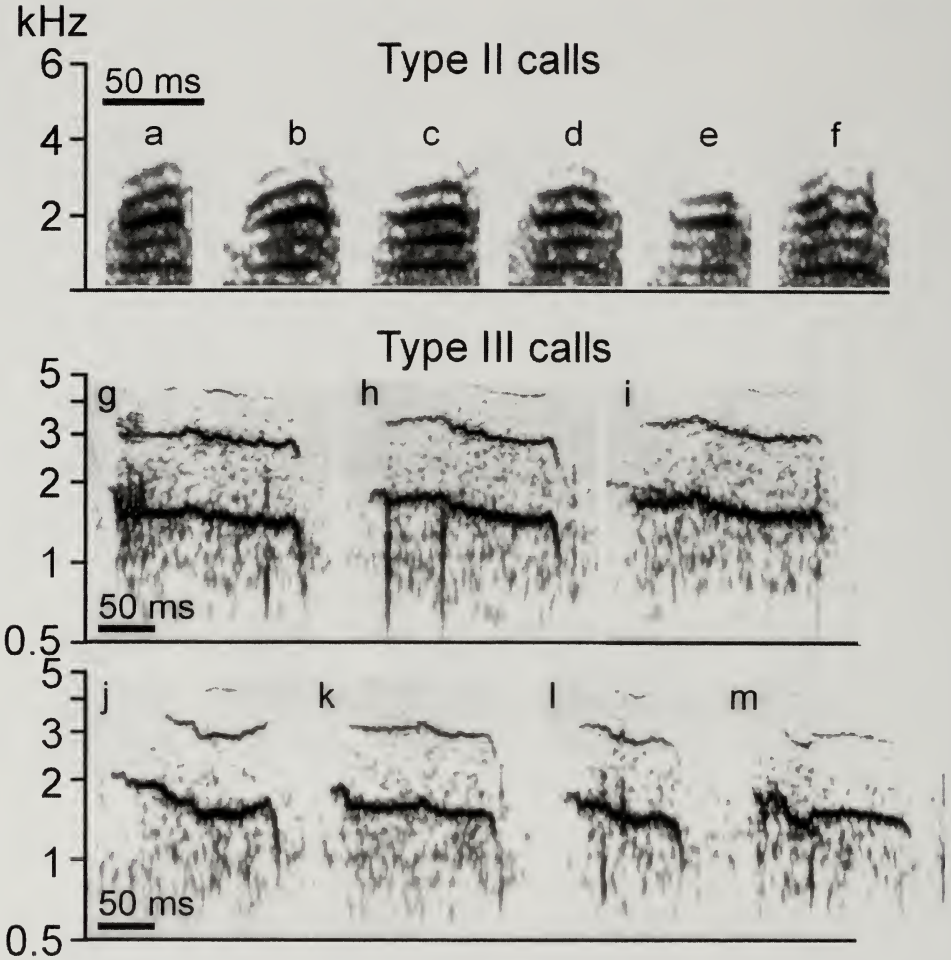

FIG. 3. Small to large differences in temporal or spectral attributes distinguish type II and type III calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre. Spectrograms a–f were produced in Raven (Blackman window, filter bandwidth = 141 Hz, grid resolution = 2.9 ms × 86 Hz); spectrograms g–m were produced in CSL 4100 (Blackman window, filter bandwidth = 63 Hz).

pitched piping or squeaky whistle uttered continuously when the bird forages" (Pratt et al. 1987:147). The apparently incessant use of this call type during foraging suggests that birds often are close to conspecifics (possibly mates, parents, or offspring), hence the call functions proximately to maintain proximity, spacing, or contact, or to inform about movement or ongoing behavior (Maier 1982, Conner et al. 2001), with ultimate functions in mate guarding or maintenance of family integrity.

Notably lacking from our sample were nuptial vocalizations that might be expected to be long, loud, repetitive, or acoustically complex, and given aerially or from a prominent display post. However, such a call type may be that described as a "joyous trill" in flight by Quayle (cited by Holyoak and Thibault 1984:77). Also, one undisturbed Tuamotu Sandpiper was observed flying slowly low (<3 m) above short vegetation, while repeating a call resembling the flight call ("tsee-wee-wee"; Hayman et al. 1986:333) of the Common Sandpiper (*Actitis hypoleucos*; Wijpkema and Wijpkema 1997, J. T. Wijpkema pers. comm.). These descriptions may refer to the same call type, which was not represented in our samples.

Quayle (cited by Holyoak and Thibault 1984:77) also described other call types, one resembling the call of a young chicken (but slightly softer) and the other a low "mih." Neither of these descriptions resembles calls we analyzed.

Prosobonia call types I and II had some syntactical organization, expressed as (1) successive grading (similarities across calls uttered in succession; e.g., initial calls in Seitres' sample 3) or (2) short trills (e.g., couplets, triplets). Successive grading is ubiquitous in trill-like calls of animals, including shorebirds (e.g., piping of *Haematopus* oystercatchers; alarm trills of calidridines; Cramp 1983; Glutz et al. 1975, 1977; Higgins 1993; Higgins and Davies 1996; Miller 1984), and intergradation from single to multi-element calls has been noted in some species (Miller 1979, Miller and Baker 1980, Conner et al. 2001). Call types I and II of *Prosobonia* resemble the latter situation, with brief, simple calls occurring individually at variable intervals or as couplets or more repetitions.

We have referred to call types I and II as being simple in structure, but simplicity and complexity are relative terms. Brief calls cannot be as structurally complex as long calls because they are temporally constrained so cannot achieve higher order temporal structure, such as complex syntax (Miller 1982). Considering their brevity, call types I and II were complex both as individual utterances and as vocal classes. First, these calls spanned an unusually large frequency range and showed strong structuring across this range (emphasized second or third harmonics also are widespread in calidridines; e.g., Cramp 1983; Glutz et al. 1975, 1977; Higgins 1993; Higgins and Davies 1996; Miller 1979, 1984). Complexity as a vocal class was increased through variation across call repetitions; frequency modulations were variably present in all parts of the call, fundamental frequency and duration varied across repetitions, and syntactical organization was expressed via sequential grading (see above).

Acoustical attributes of *Prosobonia* vocalizations suggest that they function mainly in short distance communication. Broadband complex spectra suffer attenuation and other changes over distance, so are most suitable as short distance signals (Bradbury and Vehrencamp 1998). Similarly, high acoustic variation (grading) is common in avian communication over short distances (Bradbury and Vehrencamp 1998; Marler 1976; Miller 1984, 1991). The latter relationship is due jointly to lack of physical degradation in sound signals over short distances, plus the great importance of extrasignal (contextual) sources of information in short distance signaling (Smith 1977, 1997). Subtle variations within vocal classes, such as variable frequency modulations in call types I and II, may be important short range communication signals (Hailman and Ficken 1996).

Call type III was recorded only from an apparent family group, so may have been uttered by young birds. In structure it resembles calls of chicks of other scolopacid species in being long, narrow in bandwidth, and (in many cases) of descending frequency when communicating "distress" (Douglas 1996; Nethersole-Thompson and Nethersole-Thompson 1979; Tikhonov and Fokin 1979; 1980). In some scolopacids, juveniles retain their chick calls until after fledging (Payne and Pierce 2002).

In our view, future research on vocal communication in *Prosobonia* should document the complete vocal repertoire and investigate functions of vocal classes and organization (e.g., in the Common Greenshank, *Tringa nebularia*, tempo of calling by itself is communicatively significant; Nethersole-Thompson and Nethersole-Thompson 1979, 1986). Knowledge of nuptial vocalizations and communication will be important for understanding the mating system. Finally, chick vocalizations and vocal development are poorly known in shorebirds but are likely to be informative about both behavioral function and phylogenetic relationships.

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Short Communications

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A Unique Ornament Display in Female Northern Cardinals

Jodie M. Jawor[1,3] and Randall Breitwisch[2]

ABSTRACT.—Females of many species of birds possess either a reduced version of male ornaments or conspicuous but hidden ornaments. No female specific ornament display has been described previously in a species with reduced or hidden female ornaments. We describe such a display in Northern Cardinals (*Cardinalis cardinalis*). The display consists of a perched female rotating her wings open to expose the red, carotenoid-pigmented underwing coverts, which are indicative of individual quality in this species. *Received 19 March 2003, accepted 21 September 2003.*

Birds are some of the most elaborately ornamented vertebrates. Many studies have addressed ornaments in males and their use in mate choice and intrasexual competition as indicators of condition or behavior (reviewed in Andersson 1994). The relatively few studies on female ornamentation present evidence that female ornaments can be used similarly in mate choice and intrasexual competition (reviewed in Amundsen 2000), yet no previous studies have described such a female specific display. Here we describe such a display in Northern Cardinals (*Cardinalis cardinalis*).

There are three gender patterns of ornamentation in birds. In the first, the sexes are monomorphic in ornamentation. In the second, less common pattern, females possess more elaborate ornamentation than males. In the third, the most common pattern, females possess a reduced version of the more elaborate male ornament. Lande (1980) developed the correlated response hypothesis to describe this last pattern. Under this hypothesis, female ornaments are not sexually selected but rather are the result of genome sharing between the sexes and strong selection for elaborate male ornamentation. Female ornaments are reduced in expression in response to natural selection (e.g., to reduce nest predation; Martin and Badyaev 1996). There has been little empirical support for Lande's correlated response hypothesis. However, there is growing support for the alternative hypothesis of sexual selection maintaining female ornamentation, even when ornamentation is reduced in expression (Amundsen 2000).

Studies on sexual selection and ornamentation focus on the signal value of ornaments within the context of mate choice. In species with subdued ornament expression in females, ornaments have been linked to aspects of quality such as body size, the ability to produce nests early in the breeding season, the ability to produce many eggs, or the ability to resist disease (Burley et al. 1992, Møller 1993, Owens et al. 1994, Amundsen et al. 1997, Roulin et al. 2000, Romero-Pujante et al. 2002). In some species with subdued female ornamentation, the ornaments are visually hidden on females, presumably as a result of natural selection. For instance, the female ornament may be relatively brightly colored feathers on the ventral surface of the wing, not visible when the bird is perched, but visible in flight. We have found no previous reports of species in which females overtly display hidden ornaments to males, as we have observed in female Northern Cardinals.

Male cardinals possess red plumage over the whole body, a tall head crest, a red-orange bill, and a large black face mask. Female cardinals are tan in overall plumage color, possess a similarly tall head crest and red-orange bill, but have a smaller, less distinct face mask and have red underwing coverts. Female face mask expression, bill color, and underwing covert color all indicate aspects of individual quality (Jawor et al. in press). Male cardinals perform a variety of physical displays during courtship that draw attention to ornaments, particularly the bright red plumage of the upper breast (e.g., song-dance display, song-flight, alert display, and territorial singing dis-

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play; Lemon 1968). No female displays of ornamentation have been described previously in cardinals (see Halkin and Linville 1999).

We observed on seven occasions female cardinals displaying their underwing plumage to males during breeding seasons between 1991 and 2002. Other researchers also have observed this display in female cardinals (N. Gray, S. U. Linville, P. M. Nealen, and L. L. Wolfenbarger pers. comm.). In this display, a female perches in an accentuated upright posture facing a male, with crest erect, while holding her wings out from her body. The wings are not fully extended but rather bent at the wrist, with primaries pointed downward. The posture is reminiscent of a person holding open a jacket. The red, carotenoid-pigmented underwing coverts are presented to the male. This posture is held for <5 s. There is no female vocalization accompanying the visual display. The lack of vocal announcement and short duration of the display likely are the reasons that we have observed this display so infrequently, despite hundreds of hours of focal observations of pairs of cardinals. The stance of the female is unlike that in a copulation solicitation display or a courtship feeding solicitation display (both given by female cardinals), as the female remains upright with her tail held straight down. During the lopsided display (Lemon 1968) a male cardinal may lift one wing while displaying the underside of the body. This display is quite different from the female display described here in that only one wing is lifted and partially extended away from the body, while the body is lowered and rotated about its axis (see Lemon 1968 for illustration).

All of the female displays we observed were given toward males. The members of one pair were both identified by band combinations during the display. For five of the remaining six displays observed, only one member of the pair was identified. Either the male or the female was identified by color bands during the display, and all five occurred within the boundaries of known territories. We observed the seventh display in a nearby unbanded population. We assume that the recipient of the display was the female's mate, but it is possible that this display was given to a male other than the mate.

We observed displays both early and late in the breeding season and during mid- to late morning. We did not observe copulations or copulation attempts following the female display, although in each instance the male approached within 1 m of the displaying female. Each male was positioned for good visibility 2–7 m away from the female when the display was performed, and each male approached the displaying female either during or within 5 s of her display. Following the male's approach, the pair left the area or moved into dense vegetation. We did not observe the male giving displays of his own during the time when a female displayed, nor was any male heard to sing. The male did not appear to investigate the displaying female's plumage upon landing near her, but it is probable that the male cardinal could see the underwing plumage from several meters away. Although during our observations of this display the male did not then feed the female, one researcher (P. M. Nealen pers. comm.) has observed this sequence of events. All displays were performed 5–8 m above ground in crowns of trees with sparse leaf cover. Displays do not appear to take place near the nest, as all observed displays were well above the mean nest height in this species. We do not know the displaying females' stage of reproduction. The observed displays occurred either early in the breeding season before we had found an active nest (although one may have been present) or later in the season in cases where we had not yet found a new nest for this repeatedly nesting species.

Additional findings with cardinals suggest that the described display may communicate information on individual quality. In females, the underwing plumage is indicative of multiple aspects of quality (body size, body condition, date of first nest produced, and reproductive success; Jawor et al. in press). Also, cardinal pairs mate assortatively by ornamentation (Jawor et al. 2003); cardinal pairs possess similar bill colors, and the redness of male upper breast plumage color is positively correlated with the redness of his mate's underwing plumage color. Assortative mating is suggestive of bidirectional mate choice, and the described female display may facilitate male assessment of this condition-dependent ornament in female cardinals. This display may be integral to the formation of new pairs.

Males display their quality to females via ornamentation, and our observations suggest a reciprocal display of female quality. For established pairs, this display also may maintain pair bonds, or provide information to males on female receptivity to copulations. Cardinals nest repeatedly during the breeding season (Filliater et al. 1994) and divorces occur both within season and during winter (JMJ and RB unpubl. data). This situation would favor the display of individual quality at multiple times during the year, even in established pairs. Some of these suggested functions could be tested with captive cardinals in aviary experiments, although this species does not thrive in captivity (L. L. Wolfenbarger and G. E. Hill pers. comm.).

It is clear that natural selection has acted in some bird species to reduce female ornamentation from the more conspicuous male expression (Burns 1998). Less appreciated is the fact that this process has yielded hidden ornaments that are not easily assessed when a female is perching, incubating eggs, or brooding nestlings. Hidden ornaments consist of brightly colored underwing coverts, primaries, secondaries, undertail body coverts, or tail feathers that are not easily observed unless the tail or wings are spread. There are many North American species of birds in which females possess ornamental coloration that is so hidden, e.g., many warblers, Pyrrhuloxia (*Cardinalis sinuatus*), Crimson-collared Grosbeak (*Rhodothraupis celaeno*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). We predict that at least some species with hidden female ornaments also possess female limited ornament displays.

Lande's (1980) correlated response hypothesis assumed that female ornaments are subdued in expression due to the influence of natural selection. We believe this assumption is warranted. However, this does not mean that subdued or hidden ornaments cannot serve as indicators of female quality under sexual selection. Hidden ornaments in female birds and, perhaps, female limited displays of these indicators of quality likely are a compromise between natural and sexual selection both acting directly on females.

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Group Copulation Solicitation Display among Female Greater Rheas

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ABSTRACT.—In this paper we report the copulation behavior of the Greater Rhea (*Rhea americana*), a species in which males defend a harem of females. We describe the females' behavior during 14 copulation events observed from 1995–1997 at Buenos Aires province, Argentina. During copulations, females performed a more active role than previously suggested. Moreover, on three occasions we observed that harem females performed a complex copulation solicitation display, forming a closed circle to attract the male. We hypothesize that this display could be a reliable signal to the male of the tendency of females to be inseminated and lay eggs communally. *Received 10 June 2003, accepted 15 August 2003.*

The Greater Rhea (*Rhea americana*) is a precocial flightless bird that inhabits grasslands and other open habitats in the southern Neotropics. Rheas, like other ratites and some tinamous, are unusual among birds in that they combine a complex mating system with uniparental care by males. Previous studies describing the mating behavior of Greater Rheas emphasized that males perform conspicuous reproductive behavior (Raikow 1969, Bruning 1974). Female behavior, however, has been poorly described, focusing mainly on egg laying. Here we describe the mating behavior of wild Greater Rheas, including a previously unrecorded copulation solicitation display performed by the females.

Early in the breeding season (August to September) male rheas compete for and defend a group of females. Harem sizes vary from 2 to >10 females (usually 4–6). The male copulates with each female in his harem at least once every 2–3 days, and the females lay their eggs in a single communal nest built by the male. The male performs all incubation and chick-rearing behaviors. Once the egg laying at a particular nest is completed, the females sometimes mate with other males (Astley 1907, Bruning 1974). Thus, this mating system combines harem (female defence polygyny) with sequential polyandry (Oring 1982, Jenni 1974).

We observed Greater Rheas at General Lavalle (36° 25′ S, 56° 56′ W), Buenos Aires province, Argentina, during the breeding seasons of 1995–1997. The study area is a temperate grassland of the flooding Pampa (Soriano 1991). The terrain is flat, low, and marshy, with most land <10 m above sea level (see description in Fernández and Reboreda 1998). We made observations from 7:00–19:00 EST from a vehicle located 100–200 m from rhea groups.

We observed a total of 14 copulations involving seven males. All copulations occurred during morning (7:00–11:30, $n = 6$) or evening (16:00–19:00, $n = 8$), and copulations lasted 1–2 min. The minimum observed time between successive copulations by the same male was 20 min. For nine copulations we monitored the group before copulation solicitation took place. In six instances the male approached an isolated female of the group while she fed and he started to perform courtship displays. These involved mostly head-bobbing, in which the male moves his head vigorously up and down (Raikow 1969). The female responded to the displaying male by lowered her head and then remaining motion-

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less. Meanwhile, the other females of the group approached the displaying pair and surrounded them closely. The male then compelled the female to rest on her tarsi by pushing and pecking her back, and he mounted her. The other females of the harem remained quiet with their heads lowered throughout the copulation event. When the copulation ended all the rheas began feeding.

During the other three copulations we observed, the females displayed, apparently to attract the male. In these cases the male was feeding while females approached one another, forming a circle near the feeding male. The circle formation began when a female approached another female closely and they both inclined the anterior of their bodies downward, lowering their necks slightly in a U-shape. The other females of the harem approached these two females quickly and closed the circle, adopting similar postures with their heads toward the inside of the circle. When all females had joined in the circle, they remained still for about 1 min. In two instances, the male initially was unresponsive to the display, but the females persisted and the male eventually approached them. When the male did respond, he approached the circle and walked around the females. He then attempted to copulate by grasping one of the females at the posterior base of her neck. He pulled that female away from the circle and, still grasping her, he mounted her. The other females approached and surrounded them, and then remained still with their heads lowered during the copulation. Once copulation ended, all the rheas dispersed and fed or walked. We were unable to determine how the male selected the particular female with which he copulated.

In five cases we encountered the group of birds just after the copulation display had begun; the other females remained within a couple of meters of the copulating pair. In one instance a second male approached the females and began to court them while the first male was copulating. The other females did not respond to the second male, and the first male interrupted the copulation and chased the second male away. The first male then returned and finished copulating with the same female.

We observed the females' copulation solicitation display on seven other occasions in which copulations did not occur. In each case the females' display was not a response to a specific stimulus by the male. In two cases the male was unresponsive to the females' display, and the females instead resumed feeding. In one case, while the female group was displaying, one female pecked another female and the group quickly dispersed. In the other four cases males and females were disturbed by our presence and moved away.

The females' group copulation solicitation display is unusual among birds and could be related to the communal nesting behavior of Greater Rheas. Courtship displays were suggested to be a stimulatory signal that favors the physiological adjustment between the sexes (Lehrman 1959). Thus, the display of Greater Rhea females could be related to their reproductive condition and could be a reliable signal to the male of the fertility status of females.

The females' display shares an aspect of those of lekking males in that the aggregation of displaying individuals apparently accentuates the effectiveness of the signal (Andersson 1994, Höglund and Alatalo 1995). Unlike lek mating systems, in which displays attract a partner, female rheas displayed after harem formation. Also, there was not a single female that monopolized copulations within harems, as with males in leks.

The group copulation solicitation display entails several costs for females. Each female within a harem must ensure that she will be fertilized in a timely fashion. Competition among females could arise from these effects since asynchrony in egg laying, particularly late egg laying, significantly reduces egg hatchability (Fernández 1998). This cost may increase if males are sperm limited, as was suggested for small passerines (e.g., Westneat et al. 1998, Nicholls et al. 2001). In this case, Greater Rhea males could allocate sperm among females, refusing to copulate in some cases, as we observed. This effect might increase the reproduction costs for individual females, and also increase insemination competition within a harem. Each female, then, could increase her benefit by excluding other females, thus reducing the cost of competition within harems. However, we rarely observed aggression or other evidence of competition

among members of the harems despite their physical proximity.

This potential for competition among females within harems could be molded by natural selection acting on male and female interests. Communal nesting has been suggested as an evolutionary strategy to reduce the male nest and chick attention costs in this species (Vehrencamp 2000). However, nesting Greater Rhea males neither build the nest nor sit on it until most of the females are ready to lay. In addition to the male benefits, females increase their fitness through egg laying synchrony as it is one of the main factors that affects hatching success (Fernández 1998). Asynchrony in egg laying extends the laying period, delays the onset of incubation, reduces hatching success of earlier eggs, and increases the risk of predation. Females may be selected to synchronize copulations as nesting progresses in order to optimize their individual fitness. Therefore, it would be beneficial to females to synchronize egg laying. It is likely that complex group copulation solicitation behavior evolved through a selective pressure to reach a high synchronization in egg laying, reducing the cost of a prolonged egg laying stage and nest exposure. In this way displaying females behaving cooperatively would be increasing their individual fitness.

The only lek bird species known where males show a cooperative display to attract females are manakins (genus *Chriroxiphia*) and the Ruff (*Philomachus pugnax*), a Eurasian sandpiper. All four *Chriroxiphia* species perform a coordinated cartwheel display involving two or more unrelated males (Foster 1977, 1981; McDonald 1989; McDonald and Potts 1994). In these species, instead of males cooperatively displaying to attract and court a female, only the dominant male achieves copulations (McDonald and Potts 1994). Also, incipient cooperation has been reported in two other manakins species (genus *Pipra*; Robbins 1985). Subordinate males in these species do not compete with the alpha male to mate with females, but they can gain inheritance rights to the displaying site.

Ruff males form associations within leks to attract females to the breeding arena (Hugie and Lank 1997). Resident males allow access of "satellite" males to the displaying court, and both males display to attract females, who may copulate with either male. The access of satellite males to the display court imposes several costs to the resident male, as satellite males may copulate with females and interfere with the resident's mating. These costs, however, are offset by the benefits derived from female preference for co-occupied courts. Thus, in this paradigmatic example, acceptance of satellite males by resident males appears to be the only evolutionary stable strategy (Hugie and Lank 1997). Similarly, female Greater Rheas could be exposed to a trade off between competition and cooperation, as females must synchronize and reduce interference to ensure adequate investment from the males. Males may increase their fitness by increasing harem size, reducing egg-laying asynchrony, and reducing between-female interference. As a consequence, female reproductive behavior might be molded by these conflicting forces between cooperation and competition for mating, mediated by males interests. Thus, Greater Rhea males could favor this cooperative behavior among females and might be responsible for its evolution.

Our observations indicate that the role of females in the mating behavior of Greater Rheas is more active than previously supposed. Also, these observations might reveal a cooperative behavior among females of the same harem. To our knowledge, this is the first description of females cooperation in a mating solicitation behavior in birds. In the other communal egg-laying ratite species, the Ostrich (*Struthio camelus*), such cooperative behavior is absent; instead there is a high rate of female-female competition. This could be due to the existence of a primary female who controls the copulations and egg laying of the rest of the females in the group (Bertram 1992). In the other ratite species where females have strong female-female competition, the Emu (*Dromaius novaehollandiae*), the male performs all incubation and chick care, but females usually monopolize copulations with the breeding male by actively excluding other females from nesting territories (Coddington and Cockburn 1995). Cooperative behavior of Greater Rhea females appears to be unique in birds, and may be the result of conflicting male and female interests in a species with uniparental male care. It is possible that other related species with these reproductive

characteristics, such as the Lesser Rhea (*Pterocnemia pennata*) or some tinamous species, might show a similar female behavior. Further studies are necessary to test this hypothesis and to clarify the adaptive function of such social behavior.

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Left-sided Directional Bias of Cloacal Contacts During House Sparrow Copulations

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ABSTRACT.—Most female birds have only a left ovary and associated oviduct. The entry to the oviduct is on the left side of the urodeum of the cloaca. This arrangement may favor males that mount females from the left during copulation if it results in sperm being placed closer to the opening of the oviduct. Therefore,

we predicted a left-sided directional bias of cloacal contacts during House Sparrow (*Passer domesticus*) copulations. Cloacal contacts from the left outnumbered those from the right 74 to 25 (3:1) during 25 bouts of copulation at 11 House Sparrow nests. While this pattern suggests that a left-sided bias in mounting by males during copulation may be related to the asymmetry of the female reproductive tract, it also might be related to brain lateralization. *Received 14 May 2003, accepted 15 August 2003.*

In most species, female birds have only a left ovary and associated oviduct. The entry to the oviduct is on the left side of the urodeum of the cloaca (King 1981). Interestingly, the erect phallus bends to the left (King 1981, Lake 1981), matching the asymmetry of the female reproductive tract in the approximately 3% of bird species that have an intromittent organ (e.g., ratites and anseriformes; Lake 1981, Briskie and Montgomerie 1997).

The lack of an obvious intromittent phallus would seem to make it more difficult for male passerines than for ratites or anseriforms to deposit semen near the oviduct (Briskie and Montgomerie 1997). However, the semen-emitting papilla that extrudes from the urodeum of the male cloaca in some passerines might act as a phallus (Wolfson 1954, 1960; Birkhead et al. 1991; Mulder and Cockburn 1993; Birkhead and Hoi 1994; Lombardo 2001) facilitating the placement of semen near the oviduct and thereby increasing the probability of successful fertilization (Biellier et al. 1961, Holleman and Biellier 1976). It also may be more difficult for females to eject semen (Davies 1983) deposited directly into or near the opening of the oviduct.

The anatomical asymmetry of female reproductive tracts also could favor male behavioral adaptations during copulation. For example, males that mount females from the left may be favored if doing so results in ejaculates being placed closer to the oviduct (Petersen et al. 2001). For example, Gerhardt (1933, in King 1981) observed male Ostriches (*Struthio camelus*) mounting females from the left and related this behavior to the asymmetry of the female reproductive tract. Cloacal contacts from the left outnumbered those from the right by 3:1 during Tree Swallow (*Tachycineta bicolor*) copulations consistent with the "directional bias in mounting" hypothesis (Petersen et al. 2001). We examined the generality of the directional bias in mounting hypothesis to birds without intromittent organs by determining the left-right pattern of cloacal contacts during House Sparrow (*Passer domesticus*) copulations.

METHODS

We observed House Sparrow copulations between 06:30 and 09:00 EST each day from 30 April to 24 May 2002. The sparrows bred in wooden nest boxes that were arranged in a grid in an old field or mounted on utility poles along roadways on the campus of Grand Valley State Univ., Ottawa County, Michigan (42° 57′ N, 85° 53′ W). We observed House Sparrows from the inside of parked vehicles and changed locations every 30–45 min to ensure that we observed as many active nests as possible each day. During observations, one field assistant transcribed the observations made by others.

House Sparrow copulations occur frequently and in conspicuous locations, and are easy to detect because they often are preceded by easily recognizable male and female precopulatory displays (Lowther and Cink 1992). Male House Sparrows attempted copulations by trying to land on the backs of females in order to make cloacal contact. Following Petersen et al. (2001), we (1) scored a copulation attempt as successful when we observed a male land on a female's back and both birds twisted their tails so that their cloacae made contact and (2) recorded whether each cloacal contact was made from the right or left side of the female's body. It was easy to determine the side from which males mounted females because females bent their tails in the direction opposite that of the male mounting position. Females rejected copulation attempts by either keeping their tails down, which prevented males from make cloacal contact, or by flying away.

We used SPSS ver. 10.0 for Windows (SPSS, Inc. 2002) to examine the data for normality and used parametric and nonparametric

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statistical tests to analyse data where appropriate.

RESULTS

We observed 99 cloacal contacts occurring during 25 bouts of copulation at 11 nest boxes (mean = 2.27 ± 1.35 SD bouts of copulation per nest box: range 1–5). Cloacal contacts per bout ranged from 1–11 (mean = 3.96 ± 3.31 SD, n = 25 bouts). No matter how the data were partitioned, cloacal contacts from the left outnumbered those from the right. During the first bout of copulation we observed at each nest box (1) initial cloacal contacts from the left outnumbered those from the right seven to two (78%; we did not record the direction of the first cloacal contact at two boxes), (2) the total number of cloacal contacts from the left outnumbered those from the right 30 to 6 (83%; $\chi^2 = 16.00$, df = 1, $P < 0.001$), (3) the proportion of contacts from the left (mean = 0.78 ± 0.32 SD) was significantly greater than that from the right (mean = 0.22 ± 0.32 SD; paired $t = 2.94$, df = 10, $P = 0.015$), (4) the total number of contacts from the left outnumbered those from the right at nine boxes (82%; sign test, $P = 0.02$), and (5) at six boxes (55%) all cloacal contacts were from the left. During 25 bouts of copulation, the total number of cloacal contacts from the left outnumbered those from the right 74 to 25 (74.7%).

DISCUSSION

House Sparrow copulations had the same left-sided directional bias in mounting as observed in Tree Swallows (Petersen et al. 2001), suggesting that this pattern might be common in birds without intromittent organs. Petersen et al. (2001) discussed several ways that a left-sided directional bias of cloacal contacts could reflect manifestations of male and female reproductive strategies and thus be adaptive. Similarly, some herpetologists (Crews 1978, Tokarz 1988, Tokarz and Slowinski 1990, Shine et al. 2000) have argued that some squamate reptiles alternately use each side of their hemipenis during copulation as a behavioral adaptation to sperm competition.

Contrary to the prediction of the directional bias in mounting hypothesis, American Avocets (*Recurvirosta americana*) and Black-necked Stilts (*Himantopus mexicanus*), charadriiforms that lack intromittent organs, each showed a right-sided directional bias in mounting behavior (Sordahl 2001). A directional bias in mounting in birds need not be solely related to the asymmetry of the female reproductive tract and sperm competition; it also could be related to brain lateralization (Vallortigara et al. 1999). A variety of studies (e.g., Güntürkün and Kesch 1987, Güntürkün et al. 2000) suggest that brain lateralization directly affects avian behavior through the use of the lateral field of the eye contralateral to the brain hemisphere that controls that behavior (Vallortigara et al. 1999). Studies of eye laterality in passerines suggest a right eye preference for object-specific cues and a left eye preference for spatial cues (Clayton and Krebs 1994). Furthermore, the left eye appears to be more reactive to "emotionally charged" stimuli (Vallortigara 2000). Perhaps the left-sided directional bias in mounting in swallows and sparrows is related to a left eye preference for (1) the spatial skills required for the balance necessary for successful copulation and (2) reactions to the "exciting" stimulus of a female soliciting copulation. Brain lateralization may be the proximate mechanism underlying the ultimate explanation for the left-sided directional bias in mounting observed in Tree Swallows and House Sparrows. Further study of this question is required because laterality in eye use may differ even in closely related species: Dark-eyed Juncos (*Junco hyemalis*) and American Tree Sparrows (*Spizella arborea*) favor their right and left eye, respectively, when scanning for predators (Franklin and Lima 2001).

Differentiating between these nonmutually exclusive explanations will require careful observations of the anatomical mechanics of avian copulation and determining (1) whether male mounting direction in birds influences the probability of fertilization; (2) if other bird species show a directional bias during mounting, and if so, whether the directional bias is related to phylogeny; and (3) the role of brain lateralization in bird behavior.

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Nests, Eggs, and Nestling Behavior of the Snowy-cheeked Laughingthrush (*Garrulax sukatschewi*) at Lianhuashan Natural Reserve, Gansu, China

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ABSTRACT.—We describe for the first time the characteristics of the nest sites, nests, eggs, and nestling behavior of the endemic Snowy-cheeked Laughingthrush (*Garrulax sukatschewi*). During May and June 2002, at the Lianhuashan Natural Reserve in central China, we found five nests in coniferous forest at an elevation of 2,850 m. All nests, built by both members of a pair, were cup shaped and built 1.2–2.8 m above the ground in the branches of spruce (*Picea* spp.) trees or willow (*Salix* spp.) shrubs. The eggs were unspotted and greenish blue. We observed one brood of three nestlings. The parents fed the nestlings at a frequency of about 7.9 times/h ± 2.8 SD, with the female performing 51.6% of the feedings. Both male and female adults removed the feces from the nest at a mean rate of 6.9 times/h. *Received 23 January 2003, accepted 23 August 2003.*

The poorly known Snowy-cheeked Laughingthrush (*Garrulax sukatschewi*) is endemic to China. It has a limited distribution in the Min Shan Mountains of southern Gansu and adjacent parts of northwestern Sichuan (Collar et al. 2001). As a result of destruction of natural temperate forest through logging and conversion to agriculture and pasture, it is inferred to have a small, declining, severely fragmented population and is listed as a vulnerable species by BirdLife International (Stattersfield et al. 1998, Collar et al. 2001).

The Snowy-cheeked Laughingthrush has been reported in a variety of forest types in the temperate zone, usually with undergrowth of bamboo (*Sinarundinaria nitida*) and scrub. It has been observed in Lintan, Zhuoni (Jone), Min Xian, Wudu, Wen Xian in Gansu, Nanping (Jiuzhaigou) and Pingwu in Sichuan since 1899 (Dresser and Morgan 1899, Shi et al. 1984, Li and Zhang 1989, Collar et al. 2001). In Gansu, it was found in the more elevated portions of the mountains in coniferous woodlands, especially where there is undergrowth of bamboo (Dresser and Morgan 1899). Li (1993) reported that this species laid three eggs and that the nest was cup shaped; however, no other details about the nest and eggs were provided. Up to now, it has been a little known species with virtually no information about its breeding behavior (Collar et al. 2001). Here we describe the features of the nests, eggs, nestlings, and nestling behavior of this species.

STUDY AREA AND METHODS

Our study area was in the Lianhuashan Natural Reserve in Gansu province of central China (34° 57′ N, 103° 46′ E). The forest occurs on north-facing slopes and some northeast- and northwest-facing slopes, at elevations of 2,600–3,600 m; only shrubs and grasses grow on the south-facing slopes. Coniferous forest, the most prevalent cover type (42%) in our study area, is dominated by spruce (*Picea asperata*) and fir (*Abies fargesii*). The other cover types are (1) coniferous-deciduous forest, including spruce, fir, birch (*Betula utilis*), and many kinds of willows (*Salix* spp.), and (2) shrublands, including willows, sea buckthorn (*Hippophae rhamnoides*), and grasses. Mean annual temperature is about 5.1–6.0° C, with a maximum of 34.0° C and minimum of −27.1° C. The climate is semi-arid, and in the higher elevations the annual precipitation is about 65 cm.

During 2002, five nests were found at about 2,850 m in the spruce-fir forests at the Lianhuashan Natural Reserve. We observed the parents' feeding behavior at one nest with three nestlings using 8×35 binoculars at distances of 7–15 m. On 3 July 2003 we caught and color banded the female and we recorded the behavior of both adults for 374 min. We made day-long observations from 6–9 July

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and on 11 July, until the nestlings fledged. We marked the nestlings with white cotton strings around the leg and took measurements following Zheng (1995). To describe the nest microhabitat, we measured the canopy cover, shrub cover, and ground cover on 10 × 10 m square plots at each nest.

RESULTS AND DISCUSSION

We found the first nest during the early stages of construction (<10 small twigs) in an 8-m tall spruce on 14 May, at a height of 2.7 m and 1.6 m out from the central trunk. On the second day we observed both the female and male bringing more material, but the nest was abandoned shortly thereafter, possibly because of our disturbance. On 27 May, we found the second nest about 150 m from the first one. This time the nest was built in a smaller (3-m) spruce touching the trunk at a height of 1.7 m. However, this nest also was abandoned on the second day.

On 1 June, about 70 m from the second nest, we found the third nest in the branches of a bushy willow about 1.2 m high. During our 2-h observation, the birds collected twigs within 5 m of the nest. The nest was completed on 6 June. On 11 and 12 June, the female laid the first and second eggs. However, on 13 June only one egg remained; it had a hole in the shell possibly made by an avian predator. As the three nests were located relatively close together and no other birds were seen in the vicinity, we concluded that the three nests were made by the same pair.

We discovered a fourth nest in the last stage of construction on 29 May in a small (about 3-m) spruce, touching the trunk at a height of 2 m. On 3 July, about 20–30 m from the fourth nest, we found a fifth nest containing three nestlings 2.5 m above the ground and 0.5 m out from the trunk. This nest had very little overhead protection, but was located where two branches of two spruce trees (about 4 m tall) overlapped, forming a substantial platform for the nest. Although the two nest sites were very close, we are not confident that they belonged to one pair.

The Snowy-cheeked Laughingthrushes we observed seemed to be especially vigilant and prone to abandon the nest during the course of nest construction. The first, second, and fourth nests were deserted not long after we discovered them.

The third nest had an inside cup diameter of 9.5 cm, an outside cup diameter of 14.2 cm, and a depth of 5.3 cm. The cup was lined with thin strands of bamboo and had an outer layer of madder (*Rubia* spp.) stems. The outer bowl of the nest was made mostly of twigs, mainly honeysuckle (*Lonicera* sp.), and a few from spruce, fir, and birch. The two eggs were unspotted greenish blue; one was 29.5 mm by 18.4 mm (5.9 g) and the other 28.6 mm by 19.1 mm (6.0 g).

Mean ground cover within five sampling plots around the nests was visually estimated to be 45% (20–60%) grass and 26% (15–60%) moss. Mean shrub cover within the plots was 53% (40–70%) from 0–1 m above ground and 68% (50–80%) from 1–5 m above ground. Mean canopy cover above the nests was 78% (60–90%) and tree density in the sampling plots around the nests was about 5.7 (4–8) trees per 100-m^2 plot.

When we found the fifth nest, it contained three nestlings of unknown age. Assuming a nestling period of about 15 days (i.e., similar to that of the Elliot's Laughingthrush, *Garrulax elliotii*, of the same area; Fan and Lian 1996), we estimate that the nestlings were about 7 days old when discovered. We made four day-long observations of the fifth nest during the nestling period. The female began her diurnal activities a mean of 10.3 min ± 9.8 SD before sunrise, and began nocturnal brooding a mean of 10.0 min ± 6.1 SD after sunset. The mean length of the active day was 884.3 min ± 3.0 SD (n = 4). On 3 July, from 10:00 to 16:14 (Beijing time), we saw the female brood the nestlings five times with a mean duration of 24.4 min ± 10.1 SD. After July 6, we did not see brooding behavior except on July 8th, when the female came back to the nest and brooded the nestlings for 13 min while it was raining. The female brooded the nestlings at night until 9 July. The male usually first arrived at the nest at 5:55 ± 2 min (SD; n = 5), and ended his activities at 20:22 ± 12 min (SD; n = 5). The male and female usually called to each other loudly near the nest at sunrise and sunset, and the calling lasted about 3–15 min. However, they usually were silent at other times, except when we measured the nestlings.

TABLE 1. The mean (± SD) body measurements of three nestling Snowy-cheeked Laughingthrushes at Lianhuashan Natural Reserve, Gansu, China, in July 2002.

Nestling age (days)	Wing (cm)	Tarsus (cm)	Tail (cm)	Body mass (g)
7	3.13 ± 0.33	2.76 ± 0.47	0.52 ± 0.41	29.70 ± 1.40
9	4.16 ± 0.34	3.08 ± 0.84	0.97 ± 0.77	34.97 ± 1.31
11	5.23 ± 0.35	3.35 ± 1.26	1.55 ± 1.21	37.40 ± 1.15
12	5.48 ± 0.30	3.48 ± 1.28	1.81 ± 1.27	39.07 ± 1.08
13	5.83 ± 0.39	3.39 ± 1.62	2.05 ± 1.60	39.17 ± 0.94
15	6.40 ± 0.38	3.53 ± 1.85	2.75 ± 1.93	38.70 ± 0.70

The nestlings were fed 521 times during 65.6 hours of observation. Both parents fed the nestlings at a combined frequency of about 7.9 times/h ± 2.8 SD. The feeding frequency increased from 3.2 times/h (on the first observation day) to 11.05 times/h (fledging day). We could identify the feeder in 94.2% of cases; the male provisioned 35.9% of the feedings while the female provisioned significantly more (58.3%; $\chi^2 = 27.82$, $P < 0.001$). Nestlings produced two kinds of feces; >90% were white fecal sacs with membranes enclosing the surface, and the others were black and tubular. Both the male and female removed fecal material from the nest at a mean rate of 6.9 times/h (350 times in 51.6 h) from 6–9 July.

Zheng and Wang (1998) reported that the Snowy-cheeked Laughingthrush's food includes insects, seeds, and berries. When we caught the female for marking, she had only earthworms in her bill. During our nest observations, earthworms ($n = 3$), wild strawberry ($n = 2$), unidentified small red berries ($n = 2$), and a green insect larva ($n = 1$) were brought to the nest. Most prey items, however, could not be identified.

Table 1 shows the mean body measurements of the three nestlings. There was no significant difference among them in the growth rates of any measured variable (Kruskal-Wallis Test, $P > 0.05$).

The nestlings stretched their wings and preened frequently, especially the day before fledging, apparently to rid the developing flight feathers of their sheaths. Fledging occurred at 07:24 on 11 July. The two largest nestlings jumped to the spruce branches outside the nest and repeatedly hopped back and forth from the branch. At 07:31 the third nestling left the nest. The nestlings perched on the branches and accepted food from their parents, frequently stretching their wings. At 08:01, they moved down to the ground.

We captured the young birds just after fledging. Their upper parts and back were grey-brown, and the bill was yellow with the upper mandible blended with brownish-black. Some natal down was still on the head, a mean of 8.6 mm in length. The primaries were black with a grayish white outer web. The tips of the tertiaries were white. The upper and under tail coverts were bright rufous. The tarso-metatarses and claws were pink. The tips of the rectrices were white, as were feathers in the auricular and lower occular areas.

Logging has been carried out in the Lianhuashan Mountains for more than 30 years, leaving the present fragmented forest landscape and posing a threat to populations of native forest birds. Nevertheless, our study area was in a relatively well-managed natural reserve where many species persist at seemingly high densities (e.g., Chinese Grouse, *Bonasa sewerzowi*; Sun et al. 2003). We found at least four breeding pairs of Snowy-cheeked Laughingthrush in 30 ha, suggesting that this species can survive in adequate numbers in the remaining patches of forest. This, and the government's ban on further logging in Gansu, are grounds for cautious optimism for the future of this rare endemic member of China's avifauna.

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Factors Related to Body Condition of Nestling Burrowing Owls in Buffalo Gap National Grassland, South Dakota

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ABSTRACT.—We analyzed the body condition of nestling Burrowing Owls (*Athene cunicularia*) at Buffalo Gap National Grassland during the summers of 1999 and 2000. In 1999, which had a wet spring, body condition was negatively related to brood size and distance from nest to colony edge. There was no relationship between body condition and brood size during 2000, which had normal precipitation. In 2000, nestlings of early arriving pairs were in better body condition than those that arrived later. The variance in body condition within a brood was not related to brood size. *Received 29 August 2002, accepted 28 February 2003.*

Burrowing Owls (*Athene cunicularia*) are declining in parts of their range, and it is important that wildlife managers understand factors associated with the health of young owls and their subsequent ability to survive and reproduce. Body condition has been used as a measure of health for a number of bird species (Chappell and Titman 1983, Hepp et al. 1986, Hohman and Taylor 1986, Wellicome 2000), and has been defined as the fitness of a particular individual relative to its present and future energy demands and activities (Owen and Cook 1977). Burrowing Owl nestlings typically show a large amount of variability in growth rates (Landry 1979, Bellocq 1997) and body condition (Wellicome 2000), largely attributable to the owl's asynchronous hatching; early nestlings get a greater proportion of food, which results in faster growth rates. In Canada, Wellicome (2000) found that supplementally fed pairs of Burrowing Owls had broods in better body condition than unsupplemented pairs during the two years of his study.

We analyzed the relationship between nest-

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ling body condition and brood size, pair arrival date on the breeding grounds, nest distance to the colony edge, and nearest neighbor distance. We also analyzed variation in body condition within brood as a function of brood size, predicting small broods should show less variation because of more equitable provisioning.

METHODS

We conducted our study from 1 April to 1 August of 1999 and 2000 in the Wall District of Buffalo Gap National Grassland in southwestern South Dakota (43° 44′ N, 102° 20′ W). The District has approximately 220 prairie dog (*Cynomys ludovicianus*) colonies that range in size from 0.5 to 700 ha, with a total area of about 4,000 ha. The study area was primarily in the Conata and Scenic Basins, both of which contain numerous prairie dog colonies. All colonies were subject to rotational grazing by domestic cattle, which has taken place on the National Grassland since 1900 (MacCracken et al. 1985a, 1985b). During the period of our research the mean temperature in 1999 was cooler (14.9° C) and the mean precipitation was greater (8.9 cm) than the 100-year mean temperature and precipitation (15.6° C and 6.1 cm) for the same months (National Climate Data Center 2000). During 2000, both temperature and precipitation (15.9° C and 7.1 cm) were closer to normal (National Climate Data Center 2000).

We searched prairie dog colonies for Burrowing Owl nests at least twice weekly by foot, all terrain vehicle, and 4 × 4 truck. We conducted surveys from 2 April to 15 June in 1999 and from 11 April to 15 June in 2000; no owls were present on the study site prior to surveys. All nest locations were recorded on geographic information system (GIS) maps provided by the U.S. Forest Service.

Counts of young owls usually were conducted at distances ≥100 m using a window-mounted spotting scope within a vehicle. We also scanned nearby satellite burrows (non-nest burrows used by the young) for activity. We spent a minimum of 15 min at each nest site, and frequently up to 45 min to get an accurate count. We visited nest sites at least twice a week but usually three to four times a week during this part of the study. We considered brood size to be the maximum number of young seen at each nest site prior to fledging.

We determined the date of arrival on the breeding grounds of individual pairs by the method of Wellicome (2000). Arrival dates for 1999 were not included in the analysis due to the unusually wet weather that prevented us from reaching some of the prairie dog colonies. We measured to the nearest meter the distance from a nest location to the edge of the prairie dog colony (i.e., the extent of the clipped vegetation). We determined the location of each nest (±5 m) with a global positioning system and incorporated them into the existing GIS. We determined nearest neighbor distance (the next closest nest site, even if that nest was located in a different prairie dog colony) using ArcView ver. 3.0 (Environmental Systems Research Institute, Inc. 1996).

We trapped Burrowing Owl nestlings from 19 June to 26 July 1999 and from 23 June to 1 July 2000. Nest sites selected for trapping were located in 21 (1999) and 16 (2000) prairie dog colonies of various sizes (1.5–700 ha). The nest was considered for trapping when the entire brood was consistently seen above ground, but before they started consistently using satellite burrows. Traps (similar to those used by Haug 1985) typically were set early in the morning or early in the evening to prevent heat-related stress. In order to obtain an accurate measure of mean body condition for a brood, only those nests at which at least one third of the brood was captured were used in the analyses; thus, two nests were excluded in 1999 but none in 2000.

We determined nestling body mass to the nearest 0.5 g with a spring scale. We also measured the length (±0.5 mm) of the culmen, tarsus, and unflattened wing chord (from flexed wrist to the end of the longest primary) to estimate structural size.

We used body mass corrected for structural size to provide a relative index of body condition for each bird (White and Bolen 1984, Ringleman and Szymczak 1985, Dufour et al. 1993, Wellicome 2000). We obtained a single measure of structural size for each individual through principal components analysis (PROC PRINCOMP; SAS Institute, Inc. 1999) on the correlation matrix of the three structural measurements (culmen, tarsus, wing chord). Results were analyzed for all nestlings trapped

and separate indices were generated for each year. The first principal component described positive covariation among the three variables (coefficients for 1999: 0.60, 0.58, 0.55; coefficients for 2000: 0.58, 0.59, 0.57, corresponding to tarsus, wing chord, and culmen, respectively) and accounted for 80.4% (1999) and 87.0% (2000) of the total original variance. Each bird's score along this axis (PC1 scores) served as the measurement of its structural size. The body condition index for each bird was then determined by using the mass residuals from the linear regression of mass on PC1. Thus, birds with positive residuals were heavier than what would be expected, and birds with negative residuals were lighter than what would be expected for that particular structural size (Wellicome 2000).

We used SAS (SAS Institute, Inc. 1999) for all statistical analyses. We tested all variables for normality and transformed to LOG(y + 1) if necessary. We used stepwise multiple regression to analyze the relation between the dependent variable mean body condition of broods and the independent variables brood size, distance to edge, nearest neighbor distance, and arrival date (2000 only). We used an entry P value of ≤ 0.15 for selecting variables to be retained in the model. The variation in body condition for different brood sizes, as expressed by the SD of the mean body condition of broods, also was examined using one-way ANOVA. We categorized brood sizes into: (1) small, two to three nestlings; (2) medium, four to five nestlings; and (3) large, six to seven nestlings. Results were considered significant at $P \leq 0.05$. Data were analyzed separately for each year due to the differences in weather and prairie dog activity.

RESULTS AND DISCUSSION

We trapped 94 burrowing owl nestlings in 1999 and 97 in 2000. Mean body condition was obtained for 26 nests in each year. Mean brood size for those nests was 4.2 (range: 1–7) and 4.6 (range: 2–8) in 1999 and 2000, respectively. The mean nearest neighbor distance and distance to edge was 255.9 m (range: 38–1,105 m) and 71.6 m (range: 14–176 m) in 1999, and 255.8 m (range: 56–997 m) and 97.3 m (range: 1–450 m) in 2000, respectively. The mean arrival date in 2000 was 23 April (range: 11 April to 4 May). Brood size (BS) and distance to edge (DE) were retained in the multiple regression model for 1999 and both were negatively related to body condition ($n = 26$; $y = 37.70 - 3.34(BS) - 5.51(DE)$; $R^2 = 0.24$, $P = 0.040$). In 2000, only arrival date (AD) was retained; pairs that arrived earlier on the nesting grounds had broods in better body condition than those that arrived later ($n = 26$; $y = 32.94 - 10.10(AD)$; $R^2 = 0.16$, $P = 0.043$). The t and P values of the individual parameters retained in the models are as follows: (BS) $t = -2.39$, $P = 0.026$; (DE) $t = -1.63$, $P = 0.116$; and (AD) $t = -2.14$, $P = 0.043$. Standard deviations of the mean body condition did not differ among brood sizes (1999: $n = 22$, $F_{2,19} = 0.42$, $P = 0.67$; 2000: $n = 24$, $F_{2,21} = 0.09$, $P = 0.92$).

Larger broods were in worse body condition than smaller broods in 1999. Brood size has been found to be negatively related to nestling growth rates (Landry 1979, Bellocq 1997). Precipitation was above normal in 1999, which may have affected how many young the adults could adequately feed. Wellicome (2000) noted that nestling mortality increased during periods of heavy rain, and especially when rain fell for several consecutive days. Adults may not be able to hunt during these events. Nests located closer to the edge had broods in better condition in 1999. Perhaps pairs nesting closer to the edge can easily shift their hunting efforts to resources off the colony if prey is depressed on the prairie dog colony.

Pair arrival date was negatively related to nestling body condition in 2000, the only year examined. Presumably, pairs that arrive earlier on the breeding grounds are able to secure good territories with more food resources than those forced to nest in marginal habitat. While not significant for our 26 nests, when analyzed as part of our overall study (Griebel 2000), there was a significant but weak positive relation between arrival date and nest location (i.e., early arriving pairs nested closer to the edge of the colony) ($n = 126$, $t = 2.07$, $R^2 = 0.03$, $P = 0.040$). Even though nearest neighbor distance was positively related to brood size and the number of young fledged per nest in 2000 (Griebel 2000), these factors were not related to body condition of nestlings. Since there were no differences in the variation in body condition in relation to brood size, brood

sizes may be adjusted early in the brood stage (e.g., by starvation): those young that survive the 10–14 days prior to emerging from the nest burrow may consist of a brood size the adults can adequately feed during a normal year.

The low amount of variation explained by the multiple regression models indicates other factors such as nearby food resources are associated with nestling body condition. Additional studies under different weather conditions and information on corresponding resource availability would be useful.

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Observations of a Live Glaucous-winged Gull Chick in an Active Bald Eagle Nest

Robert G. Anthony[1,3] and John T. Faris[2]

ABSTRACT.—We report an apparent nonlethal predation attempt on and subsequent adoption of a Glaucous-winged Gull (*Larus glaucescens*) chick by a pair of Bald Eagles (*Haliaeetus leucocephalus*) in the Aleutian Archipelago, Alaska. To the best of our knowledge, this is the first report of a live Glaucous-winged Gull chick in a Bald Eagle nest. We describe our observations of this occurrence and offer explanations on how it may have occurred. *Received 10 May 2003, accepted 26 July 2003.*

The occurrence of live young of other species in Bald Eagle (*Haliaeetus leucocephalus*) nests has been reported previously. There are at least four accounts of live Red-tailed Hawks (*Buteo jamaicensis*) being raised in Bald Eagle nests (Stefanek et al. 1992; Watson et al. 1993; Watson and Cunningham 1996; F. Isaacs pers. comm.). In each of these cases the authors reported that the young Red-tailed Hawks came to be in Bald Eagle nests as a result of nonlethal predation attempts and subsequent adoption of the hawk by the pair of eagles. Here we report on the unusual occurrence of a live Glaucous-winged Gull (*Larus glaucescens*) chick in a Bald Eagle nest on Amchitka Island, western Aleutian Archipelago, Alaska.

On 16 June 2002, we surveyed Bald Eagle nests on Amchitka Island (51° 22′ N, 179° 18′ E) in the western Aleutian Islands, Alaska, to describe productivity and diets. The weather was cloudy with light rain, typical of the Aleutian Islands during summer. We were surveying the coastline between Makarius Cove and South Bight on the Pacific Ocean side of the island when we encountered an active Bald Eagle nest on an isolated sea stack (a rock pinnacle in the intertidal zone). There were two adult Bald Eagles at the site, one perched on the nest and the other perched on the shoreline nearby. Upon climbing to the nest we found one eagle nestling and a live Glaucous-winged Gull chick in the nest cup. The eagle nestling weighed 4.2 kg and was partially feathered. We estimated the eaglet's age at about six weeks, based on the descriptions in Stalmaster (1987:67–69). The gull chick weighed <50 g, was covered with natal down, and was estimated to be about one week old according to the photograph and descriptions by Drury (1984:142). Based on a 26- to 27-day incubation period for Glaucous-winged Gulls (Drury 1984), we estimated that incubation of the gull egg began approximately 12 May and it hatched about 9 June. Based on the age of the eaglet and a 35-day incubation period (Stalmaster 1987:57), we estimated that the eaglet hatched during the first week of May, a few days before the egg containing the gull chick was laid. At the edge of the nest cup were the prey remains of an adult Glaucous-winged Gull, a Tufted Puffin (*Fratercula cirrhata*), a Norway rat (*Rattus norvegicus*), and an unidentified auklet (*Aethia* sp.).

We were intrigued by these observations because of the harmonious relationship between the eaglet and gull chick and the possible circumstances under which a live gull chick would come to be in an eagle nest. The gull chick was peeping and active on the nest, so JTF captured and held the gull chick while RGA weighed, measured, and banded the eaglet. When we were finished measuring the eaglet, we released the gull chick, and it immediately ran to the eaglet and sought cover under its wing. The eaglet willingly provided shelter for the gull chick with brooding-like behavior. The gull chick was healthy, sug-

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gesting that it was either being fed by the adult eagles or was scavenging enough food from the nest to survive. Because young gull chicks typically acquire food from their parents by touching their bills with their beaks (Drury 1984), we suspect that the eagles had actually adopted the young and were feeding it. We were surprised by this relationship, because adult Bald Eagles often prey on subadult or adult Glaucous-winged Gulls in the Aleutian Islands (Anthony et al. 1999).

Skutch (1976) reported on interspecific adoption in passerines, including Winter Wrens (*Troglodytes troglodytes*) that adopted Great Tit (*Parus major*) chicks, Carolina Wrens (*Thryothorus ludovicianus*) that adopted Great Crested Flycatcher (*Myiarchus crinitus*) chicks, Scarlet Tanagers (*Piranga olivacea*) that adopted Chipping Sparrow (*Spizella passerina*) chicks, and Song Sparrows (*Melospiza melodia*) that adopted American Robin (*Turdus migratorius*) chicks. In each of these cases, the chicks were fed by the breeding males while the females were still incubating their own eggs; the unrelated chicks were neglected as soon as the breeding pair's own chicks hatched.

The most intriguing question is how a live gull chick came to be in an active eagle nest and developed a harmonious relationship with the eaglet. We can think of three possible explanations: (1) the eagle nest was parasitized by a female Glaucous-winged Gull and the Bald Eagles incubated the egg to hatching, (2) the eagles preyed upon an adult female gull with a well developed egg in its oviduct and incubated the egg after the gull was consumed, or (3) one of the adult eagles captured the gull chick, delivered it to its nest as prey, and the chick survived the ordeal (i.e., a nonlethal predation attempt).

The first explanation is highly unlikely, because the gull would have laid its egg in the eagle nest during the first week of the eaglet's life, a time when the adult eagles are highly attentive and brood the young almost continuously (Stalmaster 1987). This likely would have been a fatal act by the gull because gulls are one of Bald Eagle's primary prey in the Aleutians (Anthony et al. 1999). In addition, gulls are not known to be brood parasites of other species, and incubation of the gull egg would have been performed by the eagles at least 3 weeks after the eagle chick had hatched. The change in hormone levels in birds after their young hatch likely would have prohibited incubation of the gull egg to hatching after their own chick had hatched.

Although intact eggs of Canada Geese (*Branta canadensis*), Rock Ptarmigan (*Lagopus mutus*; RGA pers. obs.) and Common Murres (*Uria aalge*; B. Moorehead pers. comm.) have been observed in Bald Eagle nests, the concurrence of a gull egg with a partially grown eaglet makes the second explanation unlikely as well. Also, Bald Eagles have been reported to eat Glaucous-winged Gull eggs in Washington (Thompson 1989).

The third explanation is not expected as Bald Eagles usually kill their prey during the initial attack, and prey are delivered to the nest dead. Nevertheless, this is the most likely explanation of the three. Death-feigning behavior of prey may contribute to the occurrence of live nestlings of other species in Bald Eagle nests.

This is not the first report of Bald Eagles tolerating or raising young of another species in their nest (Stefanek et al. 1992; Watson et al. 1993; Watson and Cunningham 1996; F. Isaacs pers. comm.). In each of these cases nonlethal predation attempts were the suspected cause of the phenomena.

In summary, we can not fully account for the manner in which a live Glaucous-winged Gull chick was in an active Bald Eagle nest, although we believe it was a result of a nonlethal predation attempt. We do not know the fate of the gull chick because our research activities on Amchitka Island were limited to two days.

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Delivery and Consumption of a Pigeon Guillemot by Nesting Northern Goshawks in Southeast Alaska

Stephen B. Lewis[1,2]

ABSTRACT.—Northern Goshawks (*Accipiter gentilis*) typically hunt in forested habitats and feed upon birds and mammals there. Relatively little is known of goshawk food habits in coastal landscapes, and few seabirds have been documented in their diets. Although guillemots (*Cepphus* spp.) are potentially available to Northern Goshawks in most coastal landscapes within its range, they have not been documented previously in this raptor's diet. I observed the delivery of a Pigeon Guillemot (*C. columba*) to a goshawk nest on a coastal island in Southeast Alaska. Guillemots forage in shallow, inshore waters, making them a potentially difficult prey item for goshawks to capture. In addition, Bald Eagles (*Haliaeetus leucocephalus*) occur in large numbers in Southeast Alaska and probably harass goshawks when they are foraging in open habitat near the beach edge. Therefore, even in areas where guillemots occur, it is likely that they are only rarely hunted by goshawks. *Received 3 April 2003, accepted 15 August 2003.*

Northern Goshawks (*Accipiter gentilis*) are opportunistic predators that consume a wide variety of bird and mammal species (Cramp 1980a, Squires and Reynolds 1997). They typically hunt in forests (Bright-Smith and Mannan 1994, Beier and Drennan 1997) where they feed on medium- to small-sized birds and mammals, including grouse, corvids, passerines, woodpeckers, and tree squirrels (Squires and Reynolds 1997). In some landscapes, however, Northern Goshawks also hunt at forest edges and the associated open habitat (Kenward 1982). Coastal landscapes provide such forest edges and intertidal habitats that are rich with marine-derived food sources that attract diverse avifauna not typically preyed upon by goshawks, e.g., shorebirds and seabirds. In this paper, I report the delivery of a Pigeon Guillemot (*Cepphus columba*) to a Northern Goshawk nest, a previously undocumented item in the goshawks' diet.

During July 1999, I observed a goshawk nest on Heceta Island (55° 45′ N, 133° 45′ W) in southern Southeast Alaska, using a video surveillance system (Lewis 2001). Heceta Island is about 18,900 ha with elevations ranging from 0–915 m. The landscape consists of coastal, temperate rain forest dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), which forms a mosaic with muskegs, alpine habitat, and extensive clear cuts in various stages of regeneration.

On 13 July, the fledgling goshawks were approximately 43 days old and were beginning to fly within the immediate vicinity of the nest. At 12:30 AST that day, an adult goshawk (sex unknown) delivered a Pigeon Guillemot to the nest. I identified this prey item

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based on three features of the carcass visible on the videotape recording: (1) a bright red leg and webbed foot, diagnostic of adult Pigeon Guillemots (Ewins 1993); (2) black feathers over the majority of the carcass, and a white wing bar; and (3) its relative size. These descriptive features do not occur in other avian species in the area (Armstrong 1995). The guillemot was approximately 65% intact upon delivery. Typically, larger prey items are missing their head and neck upon delivery, and often have been eviscerated (pers. obs.). At the nest, one juvenile goshawk began to eat the guillemot until another delivery occurred 20 min later. Intermittent feeding continued over the next two days and the carcass was gone from the nest by the third day.

Guillemots are found along both the North Pacific and the North Atlantic coasts (Cramp 1980b, Ewins 1993), where their ranges overlap with that of Northern Goshawks (Cramp 1980a, Squires and Reynolds 1997). Guillemots inhabit rocky coasts and inshore waters (Ewins 1993), and are available to avian predators in these locations (Nelson 1991, Hayward et al. 1993). Few researchers have examined the diet of goshawks in such coastal areas (Myrberget 1989, Ethier 1999), and prior to my study, none have documented guillemots in the diet. Because goshawks rarely scavenge prey (Squires and Reynolds 1997), this guillemot likely was killed by the goshawk prior to its delivery to the nest.

Northern Goshawks typically forage in forests characterized by a dense canopy, large trees, and open understory (Beier and Drennan 1997). Goshawks have broad wings and long tail that allow them to maneuver effectively in forests (Squires and Reynolds 1997) as well as ambush prey in more open habitats (Wattel 1981). In some landscapes, goshawks frequently forage along forest edges and into adjacent open habitat (Kenward 1982, Iverson et al. 1996).

Within the Alexander Archipelago of Southeast Alaska, there are thousands of kilometers of forest edge along the beach where old growth forest abuts the intertidal regions. Northwestern Crows (*Corvus caurina*), a known goshawk prey species, are strongly associated with these intertidal areas and beach fringe forests (Verbeek and Butler 1999), and goshawks readily prey upon these corvids here. While the extensive beach edge supports abundant potential prey, goshawks apparently use this resource only rarely (Lewis 2001). Goshawks are ambush predators, and forested areas provides hiding cover from which to initiate predation attempts (Squires and Reynolds 1997). In one study goshawks selected foraging sites based on habitat characteristics, not prey abundance (Beier and Drennan 1997). Foraging away from forested areas could cause goshawks to lose the advantage of surprise and likely lower their hunting success.

The behavior of Pigeon Guillemots makes them difficult for Northern Goshawks to catch away from beach edge forests. Pigeon Guillemots nest in crevices and cavities on cliffs and among boulders, usually ≤30 m from mean high tide (Ewins 1993). They often nest in small colonies that provide increased predator vigilance because more birds scan for predators (Ewins 1993). There are two known Pigeon Guillemot colonies on Heceta Island (U.S. Fish and Wildlife Service 2003), 3.5 km and 4.1 km from the goshawk nest.

Pigeon Guillemots forage in relatively shallow inshore waters, usually near their nesting areas (Kuletz 1983, Ewins 1993). Potential guillemot foraging areas are located in all directions from the goshawk nest on Heceta Island, and are located well within the home ranges of adult goshawks that were radio tagged and monitored while nesting at this site (Alaska Dept. of Fish and Game unpubl. data). However, guillemots forage away from the forest edge from which a goshawk typically would begin a predation attempt. In addition, guillemots often retreat to the ocean when a predator is detected, diving to escape (Ewins 1993).

Another potential reason goshawks generally do not forage on birds in the intertidal habitat is harassment and predation by Bald Eagles (*Haliaeetus leucocephalus*). Bald Eagles are strongly associated with beach fringe forests and the associated open habitat (Jacobson and Hodges 1999). Anecdotal evidence suggests that eagles harass and even prey upon goshawks and other raptors foraging in these intertidal habitats. In Southeast Alaska, Bald Eagles have a large, dense breeding population (Jacobson and Hodges 1999) and might limit goshawk use of intertidal areas.

Northern Goshawks prey opportunistically upon species other than those readily available to them in forested habitats. Although seabirds may be abundant in intertidal areas, they cannot be captured as effectively as birds in forest conditions. Therefore, this prey resource apparently is only rarely used by goshawks.

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White-necked Puffbird Captures Rufous-tailed Hummingbird

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ABSTRACT.—Diets of puffbirds and mortality sources of adult hummingbirds are poorly known. I observed a White-necked Puffbird (*Malacoptila macrorhynchus*) attack and capture a Rufous-tailed Hummingbird (*Amazilia tzacatl*) in the Republic of Panama. This is the first report of birds as prey of puffbirds and identifies another source of natural mortality for hummingbirds. *Received 6 October 2002, accepted 24 November 2003.*

The diets of Neotropical puffbirds are poorly known, although most are thought to be primarily insectivorous (Rasmussen and Collar 2002). Puffbirds are sit-and-wait predators that scan their surroundings then quickly sally to catch perched arthropods such as cicadas, beetles, moths, roaches, katydids, and spiders (Wetmore 1984). Some proportion of the diet includes small vertebrates, particularly lizards and frogs (Wetmore 1984), but the importance of vertebrates as prey of puffbirds has not been quantified. Birds have not previously been reported as prey of puffbirds.

On 20 December 1999, I was observing hummingbirds near a sugar water feeder in Gamboa, Republic of Panama (09° 10′ N, 79° 45′ W) at approximately 10:00 EST. Skies were partly cloudy with little wind at this forest edge. Two adult Rufous-tailed Hummingbirds (*Amazilia tzacatl*), common in second growth habitats (Robinson et al. 2000), were foraging intermittently at the feeder, which was hanging from the eave of a house located 15 m from the edge of a woodlot. One male perched on an exposed, thin dead branch, about 12 m above the ground and 5 m below the canopy of the tree in which it sat. The bird was preening with its head down when an adult White-necked Puffbird (*Malacoptila macrorhynchus*) darted from a concealed perch in the canopy of a tree 15 m away, snatched the hummingbird off its perch, and carried the hummingbird, which was uttering high-pitched distress calls, crosswise in its bill and out of sight. I was unable to observe how the puffbird might have killed and consumed the hummingbird.

Sources of hummingbird mortality are poorly understood probably because of the small size of most species. Several reported hummingbird mortality sources, for instance, are rather unusual among birds, such as entrapment in spider webs (Graham 1997), capture by insects such as praying mantis (Butler 1949, Hildrebrand 1949, Murray 1958), capture by frogs (Monroe 1957, Norris-Elye 1944) and even fish (Lockwood 1922). Their small size may predispose hummingbirds to opportunistic attack by predators whose typical prey include taxa approximately the size of hummingbirds. Reports of predation on hummingbirds by other bird species usually involve either small raptors, such as Merlins (*Falco columbarius*; Lowery 1938), American Kestrels (*F. sparverius*; Mayr 1966), or Sharp-shinned Hawks (*Accipiter striatus*; Peeters 1963). In the tropics, the Tiny Hawk (*A. superciliosus*) may be a frequent consumer of hummingbirds (Stiles 1978), whereas the Bat Falcon (*F. albogularis*) may take hummingbirds less often (Beebe 1950). Occasional reports of other bird species attacking hummingbirds include those normally known for capturing large insects as prey. Gray Kingbirds (*Tyrannus dominicensis*; Seutin and Apanius 1995), Baltimore Orioles (*Icterus galbula*; Wright 1962), Brown-crested Flycatchers (*Myiarchus tyrannulus*; Gamboa 1977), and Roadrunners (*Geococcyx californianus*; Spofford 1976) all have been observed attacking and killing hummingbirds. My observation of a White-necked Puffbird apparently is the first report of a Buconnid attacking a hummingbird. The accumulation of anecdotal observations of predation events on adult hummingbirds, such as this one, adds to our knowledge of the diversity of avian mortality risks and avian diets.

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Cactus Fruits May Facilitate Village Weaver (*Ploceus cucullatus*) Breeding in Atypical Habitat on Hispaniola

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ABSTRACT.—The Village Weaver (*Ploceus cucullatus*) usually is found in moist areas, breeding near water during the rainy season. On Hispaniola I observed the Village Weaver breeding in the desert, despite a lack of rain, and consuming the fruits of a columnar cactus (*Stenocereus hystrix*). I propose that the carbohydrate and, especially, water content of these fruits is a substitute for rainfall, facilitating Village Weaver breeding in an arid environment. Weavers also may disperse the cactus seeds. *Received 3 February 2003, accepted 25 July 2003.*

The Village Weaver (*Ploceus cucullatus*, Ploceidae) is native to Africa but has been naturalized on Hispaniola (Lahti 2003). It nests in often dense colonies in a variety of habitats, most abundantly near agricultural fields and water sources. Rice, when available, is the most significant item in the bird's diet; consistent availability of suitable grains, especially during the breeding season, has been suggested to be an important factor limiting the size of Village Weaver populations (Da Camara-Smeets and Manikowski 1981, Adegoke 1983). The species is thought to be absent from arid habitats; in fact, its native range in sub-Saharan Africa coincides with that portion of the continent which receives >35 cm per year (Lahti 2003). Rain is important in initiating colony formation and establishing subsequent breeding synchrony within the colony (Hall 1970), and the length of the rainy

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season determines the length of the breeding season (Da Camara-Smeets 1982). Here I report an observation of Village Weavers breeding in arid habitat and propose that breeding may be facilitated by consumption of cactus fruits.

During May and June 2001, I observed Village Weavers breeding in the desert of central Monte Cristi province of the Dominican Republic (19° 40′ N, 71° 10′ W), where no rain fell for at least one month. Local watercourses were dry and covered with cacti, and there were no standing water or agricultural fields in the vicinity of the breeding weavers. I located three large, dense colonies of approximately 70, 70, and 150 nests; one small colony of 8 nests; and one large diffuse colony of about 100 nests in trees of various species among stands of columnar *pitayo* cactus (*Stenocereus hystrix*). Cacti were densely distributed beneath and within 5 m of weaver nesting trees. All weaver aggregations contained birds building nests, displaying, incubating eggs, and feeding nestlings. During May and June 2001, I estimated that 70% of nests in all colonies were active.

I observed Village Weavers feeding consistently on the numerous ripe ovoid fruits of the cacti. The birds peeled and splayed open the fruits, and consumed pulp and juice along with the embedded seeds. Droppings from the weavers were frequent and distributed liberally over the ground and foliage beneath the colonies, especially from birds perched or flying within nesting trees. Droppings were watery, were colored red like the cacti fruit, and contained small, black, intact seeds that were similar in appearance to those of the cacti. The intact nature of the seeds and the apparently clumped distribution of the cacti around nesting trees raises the possibility that weavers may disperse the seeds of *Stenocereus*, as has been suggested of other birds (Wendelken and Martin 1988). I saw no other birds in the vicinity of the weaver nesting trees and cacti.

There are no previous reports of weavers feeding on cacti. Weavers might compensate for the low availability of grains in the desert by exploiting the carbohydrate-rich *Stenocereus* fruit. Fruits of other cacti, such as saguaro (*Carnegeia gigantea*) and prickly pear (*Opuntia* spp.) provide important sources of carbon and minerals to birds in other arid habitats (Everitt and Alaniz 1981, Wolf et al. 2002). If the nutritional value of *Stenocereus* is similar to that of other cacti, these weavers need to supplement their diet with protein sources such as arthropods, which are part of this bird's diet in its native range (Adegoke 1983).

Perhaps more important than nutritional value is the water source this fruit provides. Cacti with similar fruits (*Opuntia*, *Carnegeia*) can retain 80% water content by mass, and are known to be important water sources for wildlife (Le Houerou 1996, Wolf et al. 2002). Because the range and timing of breeding in the Village Weaver strongly depend upon rainfall and proximity of water sources, I suggest that the existence and breeding of this species in such an arid environment are facilitated by the water content of *Stenocereus*. Captive Village Weavers will breed all summer long despite a lack of rain, if humans provide a consistent food and water supply (Collias and Collias 1970). In natural populations, succulent fruits may substitute for rainfall in an otherwise unsuitable habitat. If this is true of *Stenocereus* and weavers on Hispaniola, breeding in this province and perhaps other arid regions of Hispaniola should coincide with the periods when *Stenocereus* fruit is ripe. Conversely, during other periods in the phenology of these cacti, weavers should cease breeding and increase their foraging range, or instead leave the deserts to establish colonies elsewhere, such as around the rice fields in central Dominican Republic. Future studies should test these predictions.

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Status of the Spotless Crake (*Porzana tabuensis*) in American Samoa

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ABSTRACT.—In July 2001, during seabird surveys in dense montane rainforest at the summit of Ta'u, we documented the occurrence of the Spotless Crake (*Porzana tabuensis*) in American Samoa for the first time in 17 years. The last sightings were made during 1985–1986 in lowland agricultural areas, semiwetland, and secondary forests. Norway rats (*Rattus norvegicus*) also were discovered in the montane forests and pose a threat to the continued survival of the crake at its only colony in the Samoan archipelago. *Received 4 June 2003, accepted 15 August 2003.*

The Spotless Crake (*Porzana tabuensis*), also known as the Sooty Rail, is present over much of the South Pacific, including Australia, New Zealand, New Guinea, the Philippines, and many oceanic islands as far east as the Marquesas Islands and Pitcairn Islands (Pratt et al. 1987). Although widely scattered in small vulnerable populations, the Spotless Crake (*P. t. tabuensis*) exists in virtually every major island group in the South Pacific. In Western Polynesia, it is extirpated from Futuna but occurs on three islands in Tonga and on six islands in Fiji (Watling 2001). It is known from Samoa only on the island of Ta'u, the easternmost high island of the Samoan archipelago. This population was discovered in 1923 when biologists with the Whitney South Seas Expedition found the birds in marshy coastal habitat on the northwestern side of the island (Murphy 1924, Banks 1984). Others were not able to find the secretive species during 1975–1976 (Amerson et al. 1982). The population was thought to be extirpated since it had not been seen since 1923 (Muse and Muse 1982), but was rediscovered during 1985, when a road-killed specimen was found. During subsequent searches one individual was seen and two more heard 1 km east of Ta'u village (Engbring and Engilis 1988). Since so much time had passed between the initial discovery and rediscovery, and these sightings were in lowland, agricultural forests in the northwestern area where the species was discovered, Engbring and Engilis (1988) speculated that the population was small and decreasing as wetland habitat diminished with a reduction in subsistence agriculture. Here we describe the discovery of crakes at the summit of Ta'u, which suggests that the population may have been larger than originally thought and that crakes could be present on other island summits in Samoa.

Ta'u (14° 14′ S, 169° 267′ W) is the largest of the Manu'a Islands located approximately 100 km east of Tutuila in the U.S. Territory

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of American Samoa. The National Park of American Samoa was established in 1993, and approximately half of the island of Ta'u was leased to the U.S. Park Service (Craig 2002). The Ta'u Island Unit encompasses 2,160 ha of coastal, upland, and high elevation scrub forests rising from the eastern and southern coastlines to the highest point in the territory at the summit of Mt. Lata (966 m). Habitat at the summit is composed of dense montane rainforest characterized by *'ie'ie* vines (*Freycinetia storkii* and *F. reinecki*), tree ferns (*Cyrtandra* spp.), native melastomes, and the invasive alien melastome (*Clidemia hirta*). Rainfall at the summit can exceed 750 cm per year and misty conditions characterize the daily weather. Hurricanes episodically modify the forest environment, and Hurricane Val destroyed much of the tree canopy on the summit in 1991.

During a seabird survey at the summit on 19 July 2001, at 08:00 (Samoan standard time) we heard calls we thought were Tahiti Petrel (*Pseudobulweria rostrata*) or Audubon's Shearwater (*Puffinus lherminieri*) chicks in burrows, but the sounds apparently moved. We marked the location and after dark we attempted to locate adults arriving to feed chicks at a burrow. Since we found no adults, we placed a voice-activated tape recorder in the undergrowth at the site, but no vocalizations were captured on tape. When we heard the calls again at 16:00 the next day, we tried to locate the bird by crawling through the tangled undergrowth of ferns and vines to the base of several tree ferns, where the sound was last heard. Although some digging had occurred under the ferns, we found no burrow or other nest. We next heard sounds from this area at about 07:30 on 21 July, and again attempted to find the calling bird in the dense vegetation. The sound moved away rapidly, suggesting a bird other than a seabird chick, which would have been unable to move so quickly in the dense undergrowth.

Our search through the tangles elicited bird movements and a rattle-like alarm call preceding the emergence of a Spotless Crake from the vegetation. Its conspicuous red eye, pink legs, and dark gray body were diagnostic. Crakes were heard again making a "bup-bup-bup-bup-bup" call from this site in December 2001 and December 2002. A "churring" call that was repeated at sunrise and sunset near our camp, about 0.5 km from the previous site, may have been from this species. Another crake was heard and glimpsed in December 2002 in similar habitat about 1.6 km distant.

Spotless Crakes are considered monogamous and territorial, possibly throughout the year (Taylor 1996). Our observations of crakes in the same area on different visits suggest crakes might be territorial year round and widely scattered through the montane forest of Ta'u, an area of about 20 km^2. Spotless Crakes occur from sea level up to 3,300 m in New Guinea (Taylor 1996). Throughout its range, they are found in rank vegetation in almost any habitat, in fern-covered hillsides, heathy flats, and coastal scrub, usually near water (Taylor 1996). On some islands, Spotless Crakes occupy low forests and also rocky habitats without standing water. They also readily occupy artificial wetlands, farmlands, and seabird islands where they have been reported to eat a wide range of prey, including insects on a cow carcass, seeds, shoots, and invertebrates, and also the eggs of shearwaters, petrels, and terns (Taylor 1996). In the Kermadec Islands, New Zealand, they have been reported foraging in trees that hold Black Noddy (*Anous minutus*) nests (Taylor 1996). On Ta'u, Tahiti Petrels are relatively common nesters in the areas where crakes were encountered, and it is possible that the crakes prey on petrel eggs.

During July 2001, we found that Norway rats (*Rattus norvegicus*) were present in moderate densities on the summit of Ta'u. Throughout the Pacific Islands, Spotless Crakes have suffered reductions and local extinctions where humans and associated exotic species are present (Taylor 1996). Crake populations in Western Polynesia are declining precipitously as a result of introduced dogs, cats, mongooses, and rats (Watling 2001). Spotless Crakes survive in rat-infested areas of New Zealand by inhabiting the wettest part of the marsh, where rats are least likely to go (C. R. Veitch pers. comm.). Similarly, crakes may persist on Fiji, despite the presence of the mongoose, by inhabiting isolated swamps (Watling 2001). As a result of rat predation, Spotless Crakes have become rare on Norfolk Island, and the species is extinct on Raoul Island in the Kermadec Island group. Spotless

Crakes persist in the Pitcairn Islands where rats have been eradicated from Oeno Island and should increase as a result (B. Bell pers. comm.). On Poor Knights Island, New Zealand, Spotless Crakes increased after human occupation ceased and pigs were removed (Taylor 1996).

Norway rats have been present at low elevations on Ta'u for many years and may have contributed to the extirpation of the Spotless Crake from these areas. Pacific rats (*R. exulans*) are common in the forest area on Ta'u, but evidently only Norway rats are established in the upper rainforest. Norway rat predation on crakes, on their invertebrate foods, and on seabirds likely is a significant threat to their survival. The climate, terrain, and fiscal and legal constraints make rat control on Ta'u summit very unlikely in the near future. Current rodenticide registration in U.S. Pacific territories does not allow usage in nonagricultural areas. An exemption from the U.S. Environmental Protection Agency (EPA) to the Federal Insecticide, Fungicide, and Rodenticide Act is being sought. The EPA and USFWS are pursuing national registrations for rodenticides (brodifacoum and diphacinone) for conservation purposes, to be used in all U.S. territories and possessions, and these should be available within several years. Even with such a registration, significant fiscal and physical barriers must be overcome to insure that the Spotless Crake, a candidate for listing under the Endangered Species Act, continues to survive in the Samoa Archipelago.

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Ornithological Literature

Edited by Mary Gustafson

THE NATURE OF NEBRASKA. By Paul A. Johnsgard. Univ. of Nebraska Press, Lincoln. 2001. 402 pp., illustrated by the author, 14 maps, 3 tables. $29.95.—Anyone interested in birds will be familiar with the many books written by Paul Johnsgard, currently a list of at least 40 titles. As each new book appears, I can't help but wonder how Dr. Johnsgard successfully continues to plow new ground. Thus it was with considerable curiosity that I delved into one of his newest, *The nature of Nebraska*. Perhaps not unsurprisingly, I was both pleased and disappointed. The book sets out to provide a comprehensive source of information about the animals and plants that might be encountered by Nebraskans and, as suggested by Johnsgard, to plant "some lasting ideas in the minds of readers" about the fauna and flora of Nebraska and their role "in the greater scheme of things." The book is based on an idea Johnsgard had after speaking to a 4th grade class, and is dedicated to "the children of Nebraska," although a read through the book suggests that it is clearly directed at a broader audience.

As one intimately familiar with Nebraska's birds, but lacking depth of knowledge of other animals and plants, I found the book to be a stimulating read and of greatest use in its discussion of the nonavian fauna and flora to be found in the various Ecological Regions of Nebraska defined by Johnsgard. Each ecological region is treated in a separate chapter; each chapter starts with a general introduction to the region, including geological information and a brief discussion of each major community existing therein. There follows a series of discussions of Keystone and Typical Species found within the ecological region. These discussions are the most interesting and useful part of the book, and can be expected to achieve Johnsgard's aim of planting "lasting ideas" in the minds of his readers. Under Ponderosa Pines and Rimrock, the ecological region found in Nebraska's far northwest, major communities described are Western Coniferous Forest, Mountain Mahogany Shrubland, and Pine Ridge Sandy-Slope Prairie. All conjure up exciting thoughts about what animals and plants one might discover there. Johnsgard does not disappoint the reader, following with evocative (a well-deserved word often used by reviewers of Johnsgard's natural history writing) and informative treatment of several species, including ponderosa pine (*Pinus ponderosa*), Prairie Falcon (*Falco mexicanus*), and mountain lion (*Felix concolor*). At the opposite end of the state lies the ecological region Johnsgard nostalgically calls The Forests of Home: the Missouri Valley and Eastern Deciduous Forest. Two of the communities of this region discussed are Southeastern Upland Forest and Eastern Floodplain Forest, and species discussed include bur oak (*Quercus macrocarpa*), fox squirrel (*Sciurus niger*), luna moth (*Actias luna*), ginseng (*Panax quinquefolius*), and Broad-winged Hawk (*Buteo platypterus*), a mix likely to arouse the curiosity of almost any reader. Johnsgard satisfies this curiosity admirably.

These sections on ecological regions are the most important part of the book and can be expected to contribute greatly to understanding by the lay public of *the nature of Nebraska*. Upon discovering, however, that these sections comprise only half of the 400-page book, I was curious about what Johnsgard had in mind for the remaining 200 pages. These consist primarily of three appendices, the first a comprehensive listing of Nebraska's fauna and flora, the second a guide to Nebraska's natural areas and reserves, and the third an index to notes of the Nebraska State Museum and items in the magazine *Nebraskaland* (published by the State of Nebraska's Game and Parks Dept.) that relate to Nebraska's natural history. Unfortunately, these appendices add considerably to the length of the book and are of little interest or even use to the average Nebraskan. There are many excellent field guides that clearly indicate which species can be found in Nebraska; these guides are readily available in the large national bookstores.

Many of the nature groups (for trees, birds, wildflowers, prairie grasslands) have guides specific to Nebraska already available. In addition, anyone interested in discovering Nebraska's wild places could simply use the excellent and readily available *Nebraska atlas and gazetteer,* published by DeLorme, which clearly shows all of the state parks, state wildlife management areas, national wildlife refuges, and federal waterfowl production areas within the state. Armed with the first half of Johnsgard's book, an appropriate field guide, and the DeLorme atlas, much could be discovered by the keen nature buff. Bare lists of species, in this case occupying all of 70 pages, are not particularly useful to persons who find themselves in a natural area and want to identify the wildlife around them.

The book concludes with a glossary, two sections of references, and an index. The glossary is lengthy, but useful and informative. The first reference section, which provides source references for each chapter of the book, is very good, and should be considered a complete bibliography to recent literature on the natural history of Nebraska. The second reference section, which lists references used in compiling the species lists, also is comprehensive and is organized by faunal and floral groups. In constructing the list of Nebraska's birds, Johnsgard used his own self-published (2000) list *The birds of Nebraska* as well as the recently published (2001) *The Nebraska breeding bird atlas,* compiled by Wayne Mollhoff. In my opinion, for various reasons, each is unsuited for the purpose, resulting in numerous inaccuracies and inconsistencies in the bird list. Consequently, one wonders whether the lists of other fauna and flora presented are up to the standards that might be expected by those with expertise in those areas. By far the most confusing aspect of Johnsgard's bird list is the absence of any definition of the terms used. While these are familiar within the birding world, the audience Johnsgard directs his book toward probably has no inkling of their meanings. Most startling is the apparently interchangeable use of "common" and "regular"; Johnsgard fails to differentiate between descriptors which refer to occurrence (regular, casual) and those referring to abundance (common, uncommon, rare). This failure leads to confusing designations of status such as those for Virginia Rail (*Rallus limicola*; "regular summer resident") and Sora (*Porzana carolina*; "common summer resident"). Which of these two species is more likely to be encountered? Another confusing term, used for several species including the Northern Goshawk (*Accipiter gentilis*), is "wintering migrant." This oxymoronic term goes unexplained. The term "local" is used without consistency; Wild Turkey (*Meleagris gallopavo*) is considered a "locally common resident" and Mississippi Kite (*Ictinia mississippiensis*) a "rare summer resident (west)," when the former breeds statewide in numbers and the latter at only one known location, Ogallala, where it is best described as locally uncommon.

Furthermore, there are several factual errors which would have been avoided with careful review. Following are a few examples among nonpasserines; a quick look suggests similar problems with the passerines. Forster's Tern (*Sterna forsteri*) is described as a "regular summer resident (west and central)" and Common Tern (*S. hirundo*) as a "regular migrant (east)." A reader could assume from this that a *Sterna* tern seen in eastern Nebraska would be a Common and one in the west a Forster's. In fact, both occur statewide in migration, but Johnsgard does not mention any migration status for the latter species. Calliope Hummingbird (*Stellula calliope*) is described as a "very rare migrant" and both Rufous (*Selasphorus rufus*) and Broad-tailed hummingbirds (*S. platycercus*) as "casual migrants", whereas the opposite is correct, and in fact Rufous Hummingbird is rather common in the Panhandle in late July and August, where it is the expected species. Barrow's Goldeneye (*Bucephala islandica*) is described as a "casual migrant"; in fact it is a regular, rare winter visitor. Great Egret (*Ardea alba*) is described as a "rare breeder," when in fact there is only one breeding record. Cooper's Hawk (*Accipiter cooperii*) is described as a "rare resident" when in fact it is a fairly common, if not common breeder. Red-shouldered (*Buteo lineatus*) and Broad-winged hawks are described as "extirpated?" even though evidence of breeding for both species has been published in the last few years.

Despite serious misgivings regarding the bird list, I recommend this book whole-heart-

edly to the audience for which Johnsgard wrote, the lay public. It is interesting to read, informative, evocative, and a handy reference for anyone venturing out into Nebraska's many and fascinating wild places. It is a pity that the book would have achieved this admirable purpose without most of the last 200 pages.—W. ROSS SILCOCK.

Wilson Bull., 115(4), 2003, pp. 495–505

PROCEEDINGS OF THE EIGHTY-FOURTH ANNUAL MEETING

SARA R. MORRIS, SECRETARY

The eighty-fourth annual meeting of the Wilson Ornithological Society was held Wednesday, 19 March, through Sunday, 23 March, 2003, in Delaware, Ohio, in joint session with the Association of Field Ornithologists and in conjunction with the Clark Ornithology Symposium. The meeting was hosted by Ohio Wesleyan University; and the Division of Wildlife, Ohio Department of Natural Resources; the Columbus Zoo and Aquarium; and the School of Natural Resources at The Ohio State University were co-hosts. Jed Burtt chaired the local committee. The local committee included a Steering Committee of Jed Burtt (chair), Ben Lawrence, Richard Phillips, Amanda Rodewald, Amy Schneider, Bill Shively, and Darlene Sillick; a Field Trips Committee of Bill Shively (chair), Amy Collins, Vic Fazio, John Watts, Danny Ingold, and Al Parker; an Equipment and Trouble-shooting Committee of Dick Phillips (chair), Chuck DeLatta, Ben Lawrence, and Trent Marburger; a Registration Committee of Charlene Howison (chair) and Pam Burtt; and a Logistics Committee of Kate Williamson and Amy Schneider. Additionally, Richard Bartmess, Gabe Below, Amy Bessette, Lauren Blyth, Louise Cooley, Sorrel Coulson, Brodie Feher, Chandra Henson, Jacob Kagey, Ben Lawrence, Erin Miller, Sarah Miller, Sarah Morris, Michelle Myers, Tiffany Opuszynski, Mike Parrish, Scott Peterson, Katie Reif, Steph Schaffner, Amy Scheider, Nikki Talianko, Kate Williamson, and Hillary Zeune provided rides between lodging and the various conference locations.

The Council met from 13:15 to 18:50 on Wednesday, 19 March, in Room 312 of the Hamilton Williams Campus Center at Ohio Wesleyan University. That evening there was an opening reception for conferees in the Benes Rooms of the Hamilton Williams Campus Center.

On Thursday, 20 March, Jed Burtt, Chair of the local committee, welcomed participants to an enchanted archipelago, the Galapagos Islands, the subject of the Sixth Clark Ornithology Symposium; and Thomas B. Courtice, President, welcomed participants to Ohio Wesleyan University. The symposium was held in the Chappelear Drama Center. That evening, the Humphries Art Hall was the site of a reception, which was followed by a banquet in the Benes Rooms of the Hamilton Williams Campus Center. At the end of the banquet, John Kricher of Wheaton College gave an inspiring talk about conservation entitled, "Galápagos as metaphor."

Participants spent Friday, 21 March, on field trips to Big Island and Killdeer Plains, Clear Creek, The Wilds, Lake Erie, or the Ohio Historical Society and Ohio Wildlife Center. All field trips converged at the Columbus Zoo and Aquarium, the site of the business meeting. After dinner Paul J. Baicich of the American Birding Association gave a thought-provoking talk on conservation entitled "Four keys to practical bird conservation in 2003."

On Saturday, 22 March, Jed Burtt, Chair of the Local Committee; Scott Sutcliffe, President of the Association of Field Ornithologists; and Ted Davis, President of the Wilson Ornithological Society, gave welcoming remarks to conferees in the Phillips Hall Auditorium on the Ohio Wesleyan University campus. Jerry Jackson provided a brief history of Bill and Nancy Klamm and their involvement with the Wilson Ornithological Society as background to their extremely generous bequest to the Society. Jed Burtt introduced Robert E. Ricklefs, of the University of Missouri–St. Louis, who presented the seventh annual Margaret Morse Nice Plenary Lecture, "The cognitive face of avian life histories."

The scientific program included 25 contributed papers organized into four paper sessions, 7 papers in the Clark Ornithology Symposium, and 32 contributed posters in addition to the Nice lecture. The committee on the scientific program was chaired by WOS Second Vice-President Doris Watt.

A social hour preceded the annual banquet in the Bayley Room of the Beeghly Library. After the dinner, President Davis briefly addressed the conferees, thanked Jed Burtt for hosting the meeting and Doris Watt and the Scientific Program Committee for a successful meeting, thanked retiring Members of Council for their service, welcomed the new Members of Council, and thanked all committee members for their hard work. At that time the awards and commendations that follow were presented. Jed Burtt thanked the local committee and all the speakers at the meeting. The meeting was adjourned at 20:56. The Ohio Wesleyan Jazz Band provided an entertaining concert following the banquet.

MARGARET MORSE NICE MEDAL
(for the WOS plenary lecture)

Robert E. Ricklefs, "The cognitive face of avian life histories."

EDWARD'S PRIZE
(for the best major article in volume 114 of *The Wilson Bulletin*)

Karl E. Miller, "Nesting success of the Great Crested Flycatcher in nest boxes and in tree cavities: are nest boxes safer from nest predation?" *Wilson Bull.*, 114(2): 179–185.

LOUIS AGASSIZ FUERTES AWARD

Ryan Norris, Queen's University, "Linking events of the annual cycle in a long-distance migratory bird using stable-carbon isotopes."

GEORGE A. HALL/ HAROLD F. MAYFIELD AWARD

(formerly the Margaret Morse Nice Award)

Liliana Naves, Universite Pierre et Marie Curie, "Female choice of young sperm in a monogamous bird: an experimental approach in Kittiwakes."

PAUL A. STEWART AWARDS

Angela D. Anders, Pennsylvania State University, "Post-breeding and post-fledging habitat use and survival of Yellow-billed Cuckoos."

Suzanne Langridge, University of California, Santa Cruz, "Crying havoc on the slug and snail: effects of riparian restoration on trophic relationships of birds and arthropods in the agriculture-riparian interface."

Marc C. Pedersen, University of Wisconsin–Milwaukee, "Extra-territorial movements of male and female Common Yellowthroats in relation to a male ornamental trait."

Daniel M. Scheiman, Purdue University, "Effects of field quality on dispersal rates of Bobolinks: a metapopulation approach."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Anna Birrenkott of Clemson University, "Investing avian vacuolar myelinopathy: a link between waterfowl and aquatic plants."

Jeffrey J. Kovatch of Syracuse University, "Trade-offs for maternal provisioning of food and heat to young House Wren nestlings."

Scott Rush of York University, "The effects of forest fragmentation on the post-fledging survival and dispersal of a forest songbird."

ALEXANDER WILSON PRIZE

(for the best student paper)

Natalie Dubois of Michigan State University, "Does cavity availability affect female mate choice or maternal investment in House Wrens."

LYNDS JONES PRIZE

(for the best student poster)

David A. Liebner of Canisius College, "Estimating stopover duration: comparing minimum stopover to estimates derived from open population models."

Selection committee for the Nice Medal—John C. Kricher (Chair), Charles R. Blem, Edward H. Burtt, Jr., William E. Davis, Jr., and Doris Watt; for the Edwards Prize—John Smallwood (chair), Richard T. Holmes, Julie Lucente, and Doris Watt; for the Fuertes, Hall/Mayfield, and Stewart Awards—James Sedgwick (chair) and Brett Peterson; for Wilson Ornithological Society Travel Awards—Doris Watt (chair); for the Wilson Prize—Leann Blem (chair), Charles Blem, Mary Brown, Dale Kennedy, Sara Morris, Craig Rudolph, John Smallwood, Doug White, and Herb Wilson; and for the Lynds Jones Prize—Leann Blem (chair), Charles Blem, Charles Brown, Dick Conner, Sandra Gaunt, and John Kricher.

BUSINESS MEETING

President Ted Davis called the business meeting to order at 18:02 in the Activities Pavilion at the Columbus Zoo and Aquarium.

Secretary Morris summarized the Council meeting on Wednesday, March 19. As of March 10, 2003, the Wilson membership stood at 1948 including 205 students. The Society also had 443 library subscriptions to *The Wilson Bulletin.* During the OSNA report, Council learned of several Wilson members who died since we last met, and Secretary Morris asked assembled members to stand while she read the following names: Dean Amadon (Tenefly, NJ), H. Lewis Batts (Kalamazoo, MI), William W. Baum (Cleveland Heights, OH), Dr. Peter Hall (St. George's, Grenada), G. Stuart Keith (Redding, CA), Nancy R. Klamm (Cleveland, OH), William A Jenner (OFallon, IL), and Simon Rositzky (Saint Joseph, MO).

The Society received several bequests in the last year including two substantial ones. The first was for $50,000 from the estate of H. Lewis Batts, a Past President of the Wilson Ornithological Society. A second bequest for approximately $1,200,000 came from the estate of William and Nancy Klamm. Bill was a longtime Treasurer of the Society, and although he predeceased his wife, Nancy was kind enough to leave the Society 40% of their estate.

During the past year, the WOS financial accounts have been moved from Mellon Bank to Merrill Lynch. Additionally, Council voted to hire Howland Capital Management to manage the assets from the Klamm estate. Council extended sincere gratitude to Allan Keith, the Chairman of the Board of Trustees, for all his work on behalf of the society during these transitions. This year, the Bentley Historical Library at the University of Michigan became the official archivist of the Society. Council is also pleased to announce that the entire run of the Wilson Bulletin is now available on-line. The University of New Mexico is hosting volumes published between 1899 and 2000, which are available free of charge. Recent volumes are available to subscribers of BioOne. The Council reelected John Smallwood as editor of *The Wilson Bulletin* for Volume 115 and elected Jim Sedgwick as editor for volume 116. The Council increased support of the Ornithological Council to $9000 from the current level of $3000. One of the most significant actions of Council was the unanimous approval of a slightly amended version of the Bylaws. Council made two minor changes to the Bylaws that were circulated to the

membership with the announcement of the meeting. First, Council changed the word ballot to vote in the first sentence of Article IV, Section 2. Second, Council added the following sentence to the end of article VII, "Amendments shall take effect at the close of the meeting at which they are approved or 30 days after the close of a mail ballot."

In 2004, the new Laboratory of Ornithology (at Cornell University) will host a joint meeting of WOS and AFO in Ithaca, NY, from April 22 to 25. Council accepted an invitation from the USGS Patuxent Wildlife Research Center and the Maryland Ornithological Society to meet with AFO and EBBA in Bowie, MD, April 21 to 24, 2005. Council also plans for the Society to participate fully in the 2006 NAOC (North American Ornithological Conference), although there is interest in having another smaller meeting in that same year.

Martha Vaughan presented the Treasurer's Report and John Smallwood presented the Editor's Report.

President Davis discussed the hard work by the Bylaws Revision Committee, which was chaired by Jay Shetterly and included Dick Banks and Ted Davis. Dick Conner moved that the Society approve the Bylaws as recommended by Council, and Toby Gaunt seconded the motion. After a discussion that future amendments should be recommended to Dick Banks, the membership unanimously voted to approve the changes (the vote was 35 in favor, 0 opposed, and 0 abstentions).

Dick Conner presented the report of the Nominating Committee, which recommended the following slate of candidates: President, Charles R. Blem; First Vice-President, Doris J. Watt; Second Vice-President, James D. Rising; Secretary, Sara R. Morris; Treasurer, Martha Vaughan; and Members of Council for 2003–2006, Robert C. Beason and Mary Gustafson. President Davis thanked the nominating committee and asked for any nominations from the floor. Hearing none, he accepted a motion to close nominations by Herb Wilson, seconded by Chan Robbins. Craig Rudolph moved that the Secretary cast a single ballot for the nominees. and Dick Conner seconded the motion, and Secretary Morris cast the ballot, electing the officers and council members.

President Davis adjourned the meeting at 18:17 after a motion from John Smallwood, which Chan Robbins seconded.

COMMENDATION

WHEREAS the Wilson Ornithological Society and the Association of Field Ornithologists celebrated the vernal equinox by holding their annual meetings in Delaware, Ohio, at Ohio Wesleyan University; and

RECOGNIZING that the Scientific Program Committee, chaired by Doris Watt and including Erica Dunn and Scott Sutcliffe, provided a thought-provoking and entertaining program of oral and poster presentations; and

RECOGNIZING that Jed Burtt organized a stimulating series of papers for the Clark Ornithology Symposium on the evolution of Galapagos birds; and

RECOGNIZING that the Committee on Local Arrangements, chaired by Jed Burtt, arranged conference venues at Ohio Wesleyan University and the Columbus Zoo, providing a comfortable, peaceful, and artistic atmosphere to learn more about birds, develop new collaborations, rekindle old friendships, and foster communication among conferees of diverse backgrounds; and

RECOGNIZING our field trip leaders and chauffeurs, provided memorable birding experiences including excellent views of raptors, waterfowl, and even a few reptiles;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and the Association of Field Ornithologists commend the Scientific Program Committee, the Committee on Local Arrangements, especially Jed Burtt, and all others who helped to make this meeting at Ohio Wesleyan a resounding success, and one that will not be forgotten.

COMMENDATION

WHEREAS William E. Davis, Jr., served the Wilson Ornithological Society as its President for the past two years with honor and distinction; and

RECOGNIZING that through his leadership the Wilson Ornithological Society has connected the past with the future by securing the Bentley Historical Library as its archivist and by ushering *The Wilson Bulletin* into the electronic era; and

RECOGNIZING that he oversaw the establishment of a process to safeguard the financial health of the Society; and

RECOGNIZING that under his command the Society reaffirmed its mission and revised its Bylaws to accurately preserve its identity and reflect its vision for the future; and

RECOGNIZING that Ted is one of the good guys;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society extends its heartfelt thanks to Ted for his leadership and friendship.

REPORT OF THE TREASURER

PROJECTED OPERATING BUDGET FOR FISCAL YEAR ENDING JUNE 30, 2003
Accepted by Council at Annual Meeting April 2002

REVISED PROJECTED OPERATING BUDGET FOR NEW FISCAL YEAR 2003
Recommended to Council at Annual Meeting in March 2003

	Budget 30 June 2002	Actual 30 June 2002	Accepted Budget 30 June 2003	Actual Six Months 31 Dec 2002	Projected Budget FY 2003
Revenue					
Direct Public Support (Contributions)	3,500	11,727	2,500	551	1,500
Bequests—Unrestricted	0	0	0	53,000	0
Membership Dues	37,000	32,232	35,000	11,603	32,000
Subscriptions	26,000	23,429	25,000	1,170	23,000
Page Charges	13,000	6,635	12,000	10,000	13,000
Royalties	1,500	1,090	1,500	231	1,000
BioOne Electronic Licensing	0	6,859	12,000	0	5,100
Sale of Back Issues & Books (Van Tyne Library)	0	2,587	500	366	1,000
Interest Income—Cash Accounts	0	1,068	800	532	1,000
Investment Income—Dividends/ Interest	0	21,273	0	9,860	20,000
Realized Gain (Loss) on Investments	0	(10,730)	0	(203)	0
Other Revenue	0	2,562	0	8	0
Total Revenue	**81,000**	**98,733**	**89,300**	**87,118**	**97,600**
Expenses					
Grants and Awards	10,900	15,380	11,000	300	10,000
Van Tyne Library—Student Salaries & Benefits	0	2,059	5,000	221	1,500
Postage & Mailing	10,000	10,248	10,000	7,743	20,000
Printing	70,000	35,112	53,500	39,177	60,000
Editor's Honorarium, Contract, Expenses (Vol. 115)	2,500	2,534	15,000	11,376	20,000
Editor's Honorarium, Contract, Expenses (Vol. 116)	0	0	0	0	10,000
Electronic Conversion	0	24,243	50,000	12,660	37,500
OSNA Management Services	10,000	13,123	14,000	3,281	13,000
OSNA Executive Director	0	2,964	2,000	741	3,000
Award Costs	0	801	0	0	1,000
Support—Ornithological Council	3,000	3,000	3,000	3,000	3,000
The Flock	5,000	0	0	0	0
Dues—American Bird Conservancy	300	150	300	0	150
Audit & Tax Preparation Fees	500	2,695	500	525	600
Office Supplies, General Postage	400	719	0	225	1,000
Storage Costs—Back Issues	0	511	3,000	0	550
Travel Expenses—Council, OSNA, NABC, OC	800	2,029	5,000	200	5,000
Insurance Expenses	0	1,805	1,000	0	1,000
Van Tyne Library Expenses	0	1,172	0	774	1,500
Membership Development	0	0	1,500	0	1,500
Investment Fees	0	3,330	2,000	1,222	2,500
Other Expenses	5,600	763	500	138	500
Total Expenses	**119,000**	**122,638**	**177,300**	**81,584**	**193,300**

Excess (Deficit)—Operating	**(38,000)**	**(23,904)**	**(88,000)**	**5,534**	**(95,700)**
Reserves Transfer for Electronic Conversion	0	0	50,000	0	37,500
Investment Transfer for Operating Deficit	38,000	23,904	38,000	0	38,000
Excess (Deficit)—After Transfers	0	0	0	5,534	(20,200)

STATEMENT OF ACTIVITIES

SIX MONTHS ENDING DECEMBER 31, 2002 (SHORT YEAR)

Revenue		**Actual**	
Direct Public Support (Contributions)	$	551.00	
Bequests—Unrestricted		53,000.00	
Memberships & Subscriptions		12,773.20	
Page Charges		10,000.00	
Royalties		230.80	
Sale of Back Issues & Books (Van Tyne Library)		366.09	
Interest Income—Cash Accounts		532.34	
Investment Income—Dividends/Interest		9,859.57	
Realized Gain (Loss) on Investments		(203.13)	
Other Revenue		8.14	
Total Revenue		**$**	**87,118.01**
Expenses			
Program Services			
Grants and Awards	$	300.00	
Van Tyne Library—Student Salaries & Benefits		221.35	
Postage & Mailing		7,743.38	
Printing & Editor's Costs		50,553.00	
Electronic Conversion		12,660.19	
OSNA Management Services		3,280.86	
OSNA Executive Director		741.00	
Support—Ornithological Council		3,000.00	
Total Program Services (96%)		$	78,499.78
Support Services			
Audit & Tax Preparation Fees	$	525.00	
Office Supplies, Postage		224.76	
Travel Expenses—Ornith. Council, OSNA, Meetings		200.00	
Van Tyne Library Expenses		774.32	
Investment Fees		1,222.12	
Other Expenses		138.25	
Total Support Services (4%)		$	3,084.45
Total Expenses		**$**	**81,584.23**
Excess (Deficit) for Six Months (Short Year)—Operating		**$**	**5,533.78**
Unrealized Gain (Loss)—Investments		**$**	**(102,477.80)**
Total Excess (Deficit) for Six Months (Short Year)		**$**	**(96,944.02)**

STATEMENT OF FINANCIAL POSITION

SIX MONTHS ENDING DECEMBER 31, 2002 (SHORT YEAR)

Assets		
Current Cash Assets		
Cape Cod Bank & Trust—Checking Account	$ 50,220.57	
Cape Cod Bank & Trust—Savings Account	51,418.75	
Merrill Lynch—Cash Account	58,079.89	
Comerica Checking—Van Tyne Account	3,824.68	
University of Michigan—Van Tyne Account	1,447.89	
Total Current Cash Assets		$ 164,991.78
Investments (Unrestricted Fund and Sutton Fund)		
Merrill Lynch—Equities	$ 703,289.00	
Total Investments		$ 703,289.00
Total Assets		**$ 868,280.78**
Fund Balances		
Fund Balances—Beginning of Fiscal Year		
Unrestricted Net Assets—Cash Accounts	$ 158,864.47	
Unrestricted Net Assets—Investments	692,991.00	
Restricted Net Assets—Sutton Fund Investments	113,369.33	
Total Fund Balances—Beginning of Year		$ 965,224.80
Current Year Change in Fund Balances		
Current Year Change in Cash Accounts	$ 6,127.31	
Current Year Change in Unrestricted Investments	(103,071.33)	
Current Year Change in Sutton Fund Investments	0.00	
Total Current Year Change		(96,944.02)
Fund Balances—End of Fiscal Year		
Unrestricted Net Assets—Cash Accounts	$ 164,991.78	
Unrestricted Net Assets—Investments	589,919.67	
Restricted Net Assets—Sutton Fund Investments	113,369.33	
Total Fund Balances—End of Year		$ 868,280.78
Total Fund Balances		**$ 868,280.78**

Martha Vaughan, *Treasurer*

EDITOR'S REPORT—2002

A total of 140 manuscripts was received during 2002. Most papers received three peer reviews (mean of 2.8). Of 417 copies sent for review, all to referees whom had accepted our invitation to review, most (94.9%) were returned: 50% within 34 days and 90% within 59 days. The most rapid response was 2 days, by e-mail. The acceptance rate was 42%, slightly higher than last year. Volume 114 consists of 52 major papers and 19 short communications. All four issues contain a color frontispiece, of which two are original paintings and two are illustrative photographs. The March and June issues each included two additional color figures, and the September issue includes one additional color figure.

Clait Braun, Richard Conner, Kathleen Beal, and Karl Miller continued to serve on the editorial board during 2002; I thank them for the many reviews they provided, and to Kathy Beal for her expert review of statistical procedures in several papers, and for compiling the index. Editorial assistants Christine Bandstra, Sophia Spadavecchia, and Matthew Zasadinski performed many of the functions of the editorial office, including receiving, acknowledging, and tracking manuscripts; contacting referees and, when necessary, reminding them to return their reviews; assembling files for my perusal; and numerous other essential operations. I am especially grateful to Julie Lucente, who performed the above functions and also helped with copy editing, and to Doris Watt, who proofread all the galleys. Montclair State University and the Department of Biology and Molecular Biology have supporting the editorial office in many ways.

At the end of summer, 2002, I informed the WOS Council of my intention to step down as editor upon completion of volume 115. I am grateful for having had the opportunity to serve WOS in this capacity, and I thank the society for the support I have received.

John A. Smallwood, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

Current members of the WOS membership committee are Jim Ingold of Louisiana State University, Chair (LA), John Smallwood of Montclair State University (NJ), Robert Sargent, Robins AFB, (GA).

Membership of Committee: We could use two additional active participants. Any suggestions on how we could gather new input are welcome. Laurie Goodrich of Hawk Mountain has resigned from the committee due to other commitments.

Chris Cudebec, Allen Press, provided data on current membership in the WOS, which is attached.

The old WOS poster was displayed at WOS meeting in Florida and at the 3rd NAOC in New Orleans during September of 2002. The newly lighted display was not yet ready for the NAOC.

Invitations for membership could not be sent to nonmembers that presented at the 2002 Wilson meeting in Florida since the request for information of participants went unanswered.

The WOS President continues to send letters of welcome to new members and letters of thanks to members upgrading their membership. Labels are provided on a monthly basis from Allen Press.

The membership chair regularly receives inquiries from members regarding the journal and the status of their membership. Most of these are received via email. Rate of messages has increased with journal lateness. All messages are responded to with explanation and forwarded to Chris Cudebec, Allen Press, as he manages the WOS database. A few people have written to get a receipt for their payment, which Chris has provided.

Anyone attending a professional meeting that could receive, set-up and tear down the WOS display please contact me. I will be happy to ship it to site location and have it shipped back to me at end of meeting. Similarly, anyone needing brochures, please contact me.

I would like to propose that organizers of the annual meeting supply the membership committee with names and address of participants notated as students and/or presenters so as to make the sending of invitations to join WOS easier.

I would also like to propose we use the current brochure as a model for creating a hanging Wilson display with tear off membership cards, for use at universities and colleges. It would be similar to the brochure in size, maybe a little larger, but on light cardboard stock, with tear off mailers. I need to get estimate on this from a printer, but could keep expenses under $500 for a test run.

Jim Ingold, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Loans:

- 88 transactions to 41 members.
- Total number of items sent was 817: 15 books lent, and 812 articles photocopied.

Acquisition of volumes:

- A total of 152 publications were received by exchange with 120 institutions.
- 22 titles were gifts from 17 organizations.
- We obtained 27 titles from 18 subscriptions. The paid subscriptions came to $729.93.
- 341 items were donated by 6 members, friends, and institutions. These donations included 15 books, 196 journal issues, 129 reprints, 10 report and 1 thesis.
- Members, friends and institutions donating materials were: Norbert Bahr, Inst. Zool. and Wildlife Res. Berlin, Clait Braun, The Peregrine Fund, C. Shackelford (Texas Parks and Wildlife), and P. W. Smith.
- New items purchased for $158.00 included 1 book, 3 journal issues, and 1 dissertation.

Dispersal of volumes:

- We sold 25 duplicate books and 236 duplicate journal issues for $1,580.84.
- We sent out 162 duplicate journal issues to L. Binford (114), Bonn Museum (14), Inst. Zool. And Wildlif Res. Berlin (24), Louisiana State University Museum (5), and Virginian Western Comm. College (5).

Accessibility on the Web:

- The web site (http://www.ummz.lsa.umich.edu/birds/wos.html) is up and running. Besides information about our holdings, we also list our books that for sale, and duplicate journal issues available for sale/trade.

We still need to reduce our stock of back issues of The Wilson Bulletin. We would like to have help from the Council in identifying libraries, people, and institutions that could benefit from getting back issues.

Thanks to: Janet Hinshaw who makes sure everything, and I mean everything, runs smoothly.

Terry L. Root, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

At the WOS meeting in 1996 in Cape May, this committee sponsored a workshop on laboratory exercises in ornithology courses. The committee is pleased to announce that many of laboratory exercises presented at that workshop are now available on the web (http://www.ummz.lsa.umich.edu/birds/WOSManual/Intro.html). Committee member Jed Burtt gets the credit for pulling these exercises together, editing them and getting them in pdf format. Thanks also to Janet Hinshaw for posting the files on the WOS web site. Jed has arranged through the Ornithological Council to have the entire manual translated into Spanish. The Spanish edition will be placed on a CD-ROM for distribution in Latin America. It will probably be distributed first at the Neotropical Ornithological Congress in Chile next fall. We hope that the CD will include the English version also.

Another workshop for the 2004 Wilson meeting is

planned with the intention of adding the resulting exercises to the on-line manual.

The Chair of the committee placed an announcement in the OSNA newsletter in the early fall asking for additions and corrections to the WOS on-line guide to graduate programs in ornithology. Feedback indicates that this guide is a useful resource for many budding ornithologists.

Herb Wilson, *Chair*

The Committee on the Scientific Program, which included Doris Watt, Erica Dunn, and Scott Sutcliffe, presented the following program of paper and poster sessions.

PAPER SESSIONS

Clark Symposium

David J. Anderson, Wake Forest University, Winston-Salem, NC, "Evolution of seabird reproductive rate."

Victor Apanius, Florida International University, Miami FL, "Immunity, self-maintenance, and the evolution of longevity in Galápagos seabirds."

Robert L. Curry, Villanova University, Villanova, PA, "Galápagos mockingbirds: the other adaptive radiation."

Kate Huyvaert and Patty Parker, University of Missouri–St. Louis, St. Louis, MO, "She said, he said: the ecology and evolution of mating behavior in the Waved Albatross."

Patty Parker and Kate Huyvaert, University of Missouri–St. Louis, St. Louis, MO, "Genetic studies of behavior and population structure in endemic Galápagos birds: implications for new diseases."

Kenneth Petren, University of Cincinnati, Cincinnati, OH, "Inferring evolutionary processes from patterns of molecular variation in Darwin's finches."

David A. Wiedenfeld, Charles Darwin Research Station, Puerto Ayora, Galápagos, Ecuador, "Up or down: three decades of population changes in the Galápagos Penguin and Flightless Cormorant."

Contributed Papers

Marja Bakermans and Amanda Rodewald, Ohio State University, Columbus, OH, "Underlying mechanisms of landscape-sensitivity of Acadian Flycatchers."

Anna Birrenkott and William Bowerman, Clemson University, PO Box 709, Pendleton, SC; Susan B. Wilde, University of South Carolina and SC-DNR, Charleston, SC; John Hains, United States Army Corps of Engineers, Calhoun Falls, SC; John Fischer, University of Georgia, Athens, GA; Thomas Murphy and Charlotte Hope, SC-DNR, Green Pond, SC; and Pamela Parnell; Clemson University, Columbia, SC; "Investigating avian vacuolar myelinopathy: a link between waterfowl and aquatic plants."

Dara G. Cantor, Lydia C. Scheidler, and Mary C. Garvin, Oberlin College, Oberlin, OH, and Kristen E. Bell, Florida International University, Miami, FL, "Patterns of northern fowl mite, Ornithonyssus sylviarum (Acarina: Mesostigmata), infestations in Gray Catbird nests."

John L. Confer, Ithaca College, Ithaca, NY, "Extirpation of Golden-winged Warblers: habitat loss and/or hybridization?"

Richard N. Conner, Southern Research Station, Nacogdoches, TX; Robert H. Johnson, Medaille College, Buffalo, NY; D. Craig Rudolph and Daniel Saenz, Southern Research Station, Nacogdoches, TX, "Do Red-cockaded Woodpeckers select cavity trees based on resin chemistry?"

Natalie S. Dubois and Thomas Getty. Michigan State University, Hickory Corners, MI, "Does cavity availability affect female mate choice or maternal investment in House Wrens?"

Mary C. Garvin and Keith A. Tarvin, Oberlin College, Oberlin, OH; Jennifer Smith, Ohio State University, Columbus, OH; Ojimadu A. Ohajuruka, Ohio Department of Health, Columbus, OH; and Sheila D. Grimes, Ohio Department of Agriculture, Reynoldsburg, OH, "Patterns of West Nile Virus infection in Ohio Blue Jays."

Marcy Heacker, Smithsonian Institution, Washington, D.C., "A study of plumulaceous feather characters of the waterfowl (Anseriformes: Anatidae)."

Siri B. Ibargüen, Ohio State University, Columbus, OH; Mark S. Woodrey, Grand Bay National Estuarine Research Reserve, Moss Point, MS; H. Lisle Gibbs, Douglas A. Nelson, and Thomas A. Waite, Ohio State University, Columbus, OH, "Geographic variation in bioacoustic, morphometric and genetic characteristics of Henslow's Sparrows: support for management units?"

Neil P. Kelley and Keith A. Tarvin, Oberlin College, Oberlin, OH, "Influence of food supplementation on nesting date in American Goldfinches."

Jeffrey J. Kovatch and F. Reed Hainsworth, Syracuse University, Syracuse, NY, "Trade-offs for maternal provisioning of food and heat to young House Wren nestlings."

Jennifer A. Mattice, Matthew M. Marshall, Duane R. Diefenbach, Pennsylvania State University, University Park, PA; Daniel W. Brauning, Pennsylvania Game Commission, Harrisburg, PA, "Grassland songbird abundance and detectability on reclaimed surface mines in western Pennsylvania."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, and Peter C. Petersen, Quad City Audubon Society, Davenport, IA, "Midwestern raptor population trends as determined by forty years of Christmas bird count data."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, and Peter C. Petersen, Quad City Audubon Society, Davenport, IA, "Using Christmas bird count data to monitor populations of icterids and species associated with humans."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL; Jon W. Stravers, Ben

R. Conklin, Ulf Konig, and Shawn Hawks, Midwest Raptor Research Fund, McGregor, IA; "Assessment of human activity impacts on Bald Eagle reproductive success along the Upper Mississippi River." Frank Price, Hamilton College, Clinton, NY, John Jungck, Beloit College, Beloit WI,, Sam Donovan and James Stewart, University of Wisconsin, Madison, WI, "The relevance of 'old' data: reexamining *Geospiza difficilis* using Lack's data from the BIRDD digital library."

Eugene S. Morton, Smithsonian Migratory Bird Center, National Zoological Park, Front Royal, VA, "Song ranging by Blue-headed Vireos."

Timothy O'Connell, Robert Brooks, Michael Lanzone, and Joseph Bishop, Penn State Cooperative Wetlands Center, University Park, PA. "Bird assemblages as indicators of ecological health on the Atlantic slope."

Rafael Rosen and Keith Tarvin, Oberlin College, Oberlin, OH, "Plumage and bill color as indicators of male quality among American Goldfinches (Carduelis tristis)."

D. Craig Rudolph, Richard N. Conner, Richard R. Schaefer, and Daniel Saenz, USDA Forest Service, Southern Research Station, Nacogdoches, TX, "Status and management of Red-cockaded Woodpeckers in Arkansas, Louisiana, Oklahoma, and Texas."

Scott A. Rush and Bridget Stutchbury, York University, North York, ON, Canada, "The effects of forest fragmentation on the post-fledging survival and dispersal of a forest songbirds."

Amy M. Schneider, Ohio Wesleyan University, Delaware, OH, "Foraging behavior of Red-bellied Woodpeckers."

Kristen L. Tettemer and Edward H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH, "A review of the use of fresh vegetation by birds as a way of limiting micro-organisms in the nest."

Andrew Vitz and Amanda Rodewald, The Ohio State University, Columbus, OH, "Post-breeding use of regenerating clearcuts by mature forest birds."

Margaret Voss and Susan Ellis, Penn State Erie, The Behrend College, Erie, PA, "Changes in maternal time allocation over the course of incubation."

Philip C. Whitford, Capital University, Columbus, OH, "Use of harassment and alarm call playback to disperse nesting Canada Geese from an Ohio business park."

POSTERS

Sara M. Agugliaro, Amanda J. Donovan, and Sara R. Morris, Canisius College, Buffalo, NY, "Accuracy of Sex Determination of Hatch-Year Common Yellowthroats (*Geothlypis trichas*) in the fall."

Kelly A. Atchison, Environmental Science Graduate Program, and Amanda D. Rodewald, The Ohio State University, Columbus, OH. "Influence of landscape matrix, microclimate, and habitat on wintering birds in riparian forests."

Penny L. Bernstein, Kent State University Stark, Canton, OH, "Laughing Gull short notes have potential to identify individuals acoustically."

Mark R. Bostrom and Gary Ritchison, Eastern Kentucky University, Richmond, KY, "Possible relationships between and among individual quality, territory quality, and hunting behavior of American Kestrels."

Sarah P. Brennan and Gary D. Schnell, University of Oklahoma, Norman, OK, "Relationships of landscape variables and breeding-bird abundance in the Central Plains."

Tammy Calvin, E. Dale Kennedy, and Doug White, Albion College, Albion, MI, "Patterns of songs used in short-range mate communication of House Wrens (*Troglodytes aedon*)."

Amy E. Collins, Ohio Wesleyan University, Delaware, OH, "Treasures from the early days of ornithology."

Louise B. Cooley, Edward H. Burtt, Jr., and Jann M. Ichida, Ohio Wesleyan University, Delaware, OH, "Microbial abundance on underweight birds."

Nicole Cotton, Karan Odom, Jann M. Ichida, and Edward H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH, "Interactions among microorganisms on the plumage of wild birds."

Matthew R. Czarnowski, Rutgers University, New Brunswick, NJ; Michael P. Lombardo, Grand Valley State University, Allendale, MI; and Harry W. Power, Rutgers University, New Brunswick, NJ, "Directional copulation bias in Tree Swallows (*Tachycineta bicolor*): male preference or female decision."

Brie Drummond, Colby College, Waterville, ME, "The selection of native and invasive plants by frugivorous birds."

Jerry Dudziak, Sara R. Morris, David L. Liebner, and H. David Sheets, Canisius College, Buffalo, NY, "Approaches to studying avian community structure during migration."

Cheryl R. Dykstra, Cleves, OH; Jeffrey L. Hays, Raptor Inc., Cincinnati, OH; F. Bernard Danniel, U.S. EPA, National Exposure Research Laboratory, Cincinnati, OH; and Melinda M. Simon, Cincinnati, OH, "Home ranges and habitat use of suburban Red-shouldered Hawks (*Buteo lineatus*)."

Janet Gorrell and Gary Ritchison, Eastern Kentucky University, Richmond, KY, "Territory size and stability in a sedentary tropical passerine: is resource partitioning a necessary condition?"

Amy Gullen, Ohio Wesleyan University, Delaware, OH, "Introduction of a female Red-bellied Woodpecker to existing aviary."

Amanda Kent and E. Dale Kennedy, Albion College, Albion, MI, "Examination of methods to increase DNA yield from feathers to determine sex ratios of nestling House Wrens (*Troglodytes aedon*)."

Amanda M. Larracuente, Melissa Mustillo, Kathryn E. Mattern, Kristen M. Covino, David A. Liebner, H. David Sheets, and Sara R. Morris, Canisius College, Buffalo, NY, "Reliable use of migration banding data: effect of sample size and capture history on Goodness-of-Fit and model selection."

David A. Liebner, Sara R. Morris, and H. David

Sheets, Canisius College, Buffalo, NY, "Estimating stopover duration: comparing minimum stopover to estimates derived from open population models."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, Peter C. Petersen, and Brian L. Blevins, Quad City Audubon Society, Davenport, IA, "Avian survey of the Savanna Ordnance Depot Bottomlands, an upper Mississippi River floodplain site."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, James P. Quinlivan, and Michael S. Bornstein, U.S. Fish and Wildlife Service, Mark Twain National Wildlife Refuge, Wapello, IA, "A comparison of avifaunal monitoring using point count and random area search methods."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, and Gregory M. Quartucci, Smith Group JJR, Madison, WI, " Influence of ice cover on Bald Eagle distribution within the upper Mississippi River region."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, and Gregory M. Quartucci, Smith Group JJR, Madison, WI, "Influence of foraging perch habitat on Bald Eagles in westcentral Illinois."

Kelly J. McKay, Niabi Biological Research and Monitoring Center, Hampton, IL, Jon W. Stravers, Midwest Raptor Research Fund, McGregor, IA, Gary V. Swenson, Casey J. Kohrt, and Joseph S. Lundh, U.S. Army Corps of Engineers, Mississippi River Project, Rock Island District, Pleasant Valley, IA, "Summary of Red-shouldered Hawk reproductive success along the upper Mississippi River Valley, 1983–1997."

Mark Monroe and Gary Ritchison, Eastern Kentucky University, Richmond, KY, "Breeding biology of Henslow's Sparrows on reclaimed surface mines in Kentucky."

Jahnvi Purwar, Ohio Wesleyan University, Delaware, OH, Jeroen Reneerkens, Royal Netherlands Institute for Sea Research, Texel, The Netherlands, Edward H. Burtt, Jr., Ohio Wesleyan University, and Jann M. Ichida, Ohio Wesleyan University, Delaware, OH, "Possible shifts in the antibacterial activity of uropygial oil that changes from monoester to diester in incubating Red Knots (*Calidris canutus*)."

Heather Reid, Colby College, Waterville, ME, "Population trends of the Northern Bobwhite, *Colinus virginianus,* in the USA from 1966 to 2001."

Jeffrey A. Spendelow, USGS Patuxent Wildlife Research Center, Laurel, MD, "Consequences of Black-crowned Night-Heron predation on Roseate Tern: population dynamics at Falkner Island, Connecticut."

Peter Stettenheim, Plainfield, NH, "What do feathers do for birds?"

Karen B. VanKuiken, Michael P. Lombardo, Patrick A. Thorpe, Grand Valley State University, Allendale, MI, "Left-sided directional bias of cloacal contacts during House Sparrow (*Passer domesticus*) copulations."

Mark Vukovich and Gary Ritchison, Eastern Kentucky University, Richmond, KY, "Nest-site selection and nesting success of Northern Harriers on reclaimed grasslands in Kentucky."

Faith E. Wiley, H. Furman Cantrell, and William W. Bowerman, Clemson University, Pendleton, SC, "Effects of bioaccumulative contaminants on intestinal flora of Bald Eagles and domestic chickens."

Kate E. Williamson, Benjamin T. Lawrence, Jann M. Ichida, and Edward H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH, "Comparison of the microbial community in the plumage of Neotropical migrants and North American residents."

ATTENDANCE

CONNECTICUT: *Beacon Falls,* Tiffany Opuszynski.

COLORADO: *Fort Collins,* James Sedgwick.

FLORIDA: *Fort Myers,* Jerome Jackson; *Miami,* Victor Apanius.

INDIANA: *Fort Wayne,* Warren Pryor.

ILLINOIS: *Chicago,* Caryn Lowther, Peter Lowther; *Hampton,* Kelly McKay.

KANSAS: *Lawrence,* Tammy Reasoner.

KENTUCKY: *Richmond,* Mark Bostrom, Janet Gorrell, Michael Hodge, Gary Ritchison, Mark Vukovich; *Winchester,* Mark Bustrom.

MAINE: *Waterville,* Brie Drummond, Heather Reid, Herb Wilson.

MARYLAND: *Chevy Chase,* Ellen Paul; *Fort Washington,* Paul Baicich; *Laurel,* Chandler Robbins, Jeff Spendelow.

MASSACHUSETTS: *Chilmark,* Allan Keith, Winifred Keith; *East Falmouth,* William Davis, Jr.; *Pocasset,* John Kricher, Martha Vaughan.

MICHIGAN: *Albion,* Tammy Calvin, Dale Kennedy, Amanda Kent, Douglas White; *Allendale,* Madeline Lombardo, Michael Lombardo, Karen VanKuiken; *Hickory Corners,* Natalie Dubois; *Niles,* Doris Watt.

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NEW HAMPSHIRE: *Plainfield,* Peter Stettenheim.

NEW JERSEY: *Randolph,* John Smallwood.

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Danny Ingold; *Oberlin,* Dara Cantor, Mary Garvin, Neil Kelley, Rafael Rosen, Keith Tarvin; *Oxford,* Chris Betrus; *Reynoldsburg,* Katie Yates; *Sandusky,* Robert Beason; *Sunbury,* Lauren Blyth; *Wilmington,* Robert Thobaben.

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PENNSYLVANIA: *Allentown,* Daniel Klem; *Cambridge Springs,* Eugene S. Morton; *Erie,* Margaret Voss; *Shreveport,* James Ingold; *Sugar Grove,* Pam Stoleson, Scott Stoleson; *University Park,* Matt Marshall, Jennifer Mattice; *Villanova,* Bob Curry.

SOUTH CAROLINA: *Pendleton,* Anna Birrenkott, Faith Wiley.

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VERMONT: *Dorset,* Betty Gilbert; *Northfield,* William Barnard.

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Location unavailable: Jill Awkerman, Umut Aypar, Paul Gledhill, Patricia Lang, Abigail Maley, Terri Manness, Scott McConnell, Ron Nyland, Laura Tuhela-Reuning, Don Watts.

ACKNOWLEDGMENTS

The following individuals graciously served as referees for this volume of *The Wilson Bulletin*. I am deeply grateful for their assistance and advice.—John A. Smallwood, Editor.

J. A. Amat, E. M. Ammon, J. G. T. Anderson, D. W. Anderson, T. R. Anderson, K. A. Arnold, J. L. Atwood, G. Aulen, M. C. Baker, R. P. Balda, J. Ball, R. C. Banks, C. D. Becker, M. Beck, J. R. Belthoff, K. S. Berg, L. B. Best, R. O. Bierregaard, R. G. Bijlsma, K. L. Bildstein, T. R. Birkhead, C. R. Blem, P. Blenginger, D. E. Blockstein, W. M. Block, W. J. Bock, R. Boettcher, E. K. Bollinger, G. R. Bortolotti, W. W. Bowerman, G. T. Braden, C. E. Braun, C. W. Breuner, J. V. Briskie, M. Britten, B. T. Brown, T. Brush, A. L Bryan, F. G. Buckley, N. J. Buckley, J. J. Buler, E. Bull, W. Busby, D. F. Caccamise, T. J. Cade, A. Chalfoun, B. R. Chapman, G. Chilton, B. Christman, C. Cicero, W. S. Clark, J. S. Coleman, C. Collins, M. Colwell, R. N. Conner, R. D. Crawford, C. Creighton, D. Cristol, A. Cruz, M. Cuadrado, C. M. Custer, T. W. Custer, C. Davis, W. E. Davis, R. H. Day, D. Delehanty, K. C. Derrickson, M. Desmond, S. DeStefano, J. G. Dickson, J. A. Donazar, C. Dove, J. Drennan, R. Drewien, R. D. Drobney, D. Duffy, L. A. Dugatkin, J. P. Duguay, J. B. Dunning, E. C. Dunn, S. W. Eaton, P. F. Elliott, D. H. Ellis, S. D. Emslie, W. Estes, L. J. Evans-Ogden, J. R. Faaborg, G. L. Farnsworth, S. F. Ferrari, M. S. Ficken, E. J. Finck, J. Fjeldsa, D. J. Flaspohler, R. Fraga, F. Fransson, K. E. Franzreb, J. D. Fraser, M. Galleti, D. E. Gawlik, R. Gerhardt, J. A. Gessaman, G. R. Geupel, J. D. Gilardi, W. M. Gilbert, H. Godinez-Alvarez, C. B. Goguen, L. J. Goodrich, W. P. Gorenzel, P. A. Gowaty, D. L. Graham, D. Granfors, G. S. Grant, P. R. Grant, C. Gratto-Trevor, C. R. Griffin, T. C., Grubb, Jr., J. Hagar, T. Haggerty, S. L. Halkin, J. Hanula, A. Harfenist, R. G. Harper, F. E. Hayes, J. Hegelbach, D. Heg, C. J. Henny, J. R. Herkert, M. Hersek, D. Hoag, K. A. Hobson, S. Hoekman, W. L. Hohman, J. Hoover, D. L. Howell, S. Howell, M. W. Hubbard, P. D. Hunt, L. Imbeau, J. L. Ingold, M. L. Isler, J. A. Jackson, J. M. Jawor, J. R. Jehl, Jr., J. E. Jimenez, P. A. Johnsgard, D. H. Johnson, J. F. Kelly, W. L Kendall, P. L. Kennedy, P. Kerlinger, S. L. Kight, N. Klaus, D. Klem, Jr., F. L. Knopf, D. E. Kroodsma, K. Kuletz, J. A. Kushlan, D. B. Lank, W. E. Lanyon, S. Latta, S. Laugheed, D. Lauten, M. L. Leonard, B. D. Leopold, L. Leschner, D. J. Levey, J. Liebezeit, J. T. Lifjeld, M. Lindberg, C. A. Lindell, P. Lonsdale, D. F. Lott, M. J. Lovallo, P. E. Lowther, G. A. Lozano, R. H. Macedo, C. G. Mahan, N. A. Mahony, M. S. Martell, D. McCrimmon, R. McNeil, K. D. Meyer, G. O. Miller, K. E. Miller, D. W. Mock, P. J. Mock, A. P. Moller, T. E. Moorman, J. L. Morrison, M. L. Morrison, T. M. Morton, H. C. Mueller, R. Norris, J. C. Ogden, L. J. E. Ogden, K. E. Omland, J. C. Ortega, J. P. O'Neill, J. F. Pacheco, G. W. Page, W. E. Palmer, J. A. Parkhurst, K. C. Parsons, B. G. Peterjohn, A. P. Peterson, D. R. Petit, K. E. Petit, L. J. Petit, P. J. Pietz, W. H. Piper, J. Pithon, M. A. Pizo, W. Post, B. Poulin, H. D. Pratt, G. A. Proudfoot, R. O. Prum, K. Purcell, J. S. Quinn, M. G Raphael, J. Rappole, J. V. Remsen, J. Reneerkens, R. E. Reynolds, R. E. Ricklefs, G. Robertson, S. Roberts, J. A. Rodgers, C. M. Rogers, D. Rollins, D. Roome, J. Roper, K. V. Rosenberg, R. Roth, S. Russo, P. G. Salaman, T. P. Salmon, F. Sanchez-Bayo, B. K. Sandercock, F. C. Schaffner, S. D. Schemnitz, J. A. Schmutz, E. A. Schreiber, M. A. Schroeder, J. H. Schulz, G. Schupp, J. A. Sedgwick, C. E. Shackelford, D. A. Shealer, A. Sheehey, L. L. Short, T. R. Simons, P. D. Smallwood, M. K. Sogge, T. Sordahl, C. Staicer, M. M. Stake, K. Steenhof, G. F. Stiles, A. M. Strong, B. J. Stutchbury, A. Suarez, G. C. Sutter, K. A. Tarvin, E. J. Temeles, J. Terborgh, M. Thery, W. E. Thogmartin, F. R. Thompson, J. Thompson, K. Titus, P. L. Tubaro, D. J. Twedt, E. K. Urban, I. Uzhaki, Q. Vega, P. D. Vickery, C. M. Vleck, G. A. Voelker, I. G. Warkentin, J. W. Watson, B. Watts, L. Weber, C. Welsh, T. Wesolowski, S. West, D. Whitacre, B. M. Whitney, C. Whittow, P. Widen, K. L. Wiebe, J. T. Wijpkema, U. Wiktander, D. E. Willard, E. O. Willis, W. H. Wilson, M. Winter, E. J. Woehler, N. Woffinden, D. Wood, R. H. Yahner, Y. Yom-tov, R. Yosef, A. Zahavi, L. Zanette, K. Zyskowski.

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by Kathleen G. Beal

This index includes references to genera, species, authors and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Nomenclature follows the AOU Check-list of North American Birds (1998). Reference is made to books reviewed, and announcements as they appear in the volume.

Abraham, Kenneth F., see Nguyen, Linh P., Erica Nol, and ———
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